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Fossil and subfossil herpetofauna from Cadet 2 Cave (Marie-Galante, Guadeloupe Islands, F. W. I.): Evolution of an insular herpetofauna since the Late Pleistocene



L'herpétofaune fossile et subfossile de la grotte Cadet 2 (Marie-Galante, Archipel de la Guadeloupe, P.-A. F.) : évolution d'une herpétofaune insulaire depuis le Pléistocène supérieur

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ABSTRACT

This study deals with the herpetofaunal fossil and subfossil remains from the Cadet 2 site (Marie-Galante, Guadeloupean Archipelago). This study provides new data concerning the herpetofaunal community since the Late Pleistocene by revealing the early local occurrence of some taxa (*Eleutherodactylus* sp., cf. *Sphaerodactylus* sp., *Ameiva* sp., cf. *Capitellum mariagalantae*, *Anolis* cf. *ferreus*, cf. *Antillotyphlops* sp., cf. *Alsophis* sp. and Colubroidea sp. 1) and possible Pleistocene extinctions (*Boa* sp. and Colubroidea sp. 2). Moreover, the first metric data for fossil Marie-Galante anoles show clear size stability throughout time. As regards the evolution of the island herpetofaunal biodiversity, our work points to the long-term stability of the fauna before human colonization and subsequently to the marked impact of human-caused environmental disturbances during colonial but also Pre-Columbian periods.

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R É S U M É

Nous étudions ici le matériel herpétofaunistique provenant du site de Cadet 2, situé sur l'île de Marie-Galante, dans l'archipel de la Guadeloupe. L'analyse de ces restes apporte des données inédites concernant le peuplement herpétologique de l'île depuis le Pléistocène supérieur. Elle met en évidence la présence ancienne de certains taxons sur l'île (*Eleutherodactylus* sp., cf. *Sphaerodactylus* sp., *Ameiva* sp., cf. *Capitellum mariagalantae*, *Anolis* cf. *ferreus*, cf. *Antillotyphlops* sp., cf. *Alsophis* sp. et Colubroidea sp. 1). Elle montre aussi de possibles extinctions datant du Pléistocène (*Boa* sp. et Colubroidea sp. 2). Nos premiers résultats

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obtenus sur les faibles variations de la taille des anolis fossiles de Marie-Galante démontrent la grande stabilité des peuplements au cours du temps. Ce travail met en avant la stabilité de l'herpétofaune de l'île durant les périodes précédant l'arrivée de l'homme, puis les modifications considérables qui suivent son installation pendant les périodes précolombiennes, puis modernes.

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1. Introduction

The biogeography of the Greater and Lesser Antilles herpetofauna has been the subject of several publications during the past decades (Hedges, 1996, 2006; Lescure, 1987; Lescure et al., 1991). Thus, the present-day composition and distribution of the herpetofauna on the Caribbean Islands is well known (Henderson and Powell, 2009; Powell and Henderson, 2012). In the same way, the modern herpetofauna on the Guadeloupe Islands is well documented and has recently been the subject of a monograph (Breuil, 2002). In contrast, the fossil and subfossil herpetofauna is poorly known, in particular in the Lesser Antilles (Pregill and Olson, 1981; Pregill et al., 1988, 1994). Many questions remain unresolved as regards the past Guadeloupean herpetofaunal community and in spite of several studies focusing on archaeological fauna (Grouard, 2001, 2003, 2007, 2010), pre-anthropogenic fossil data for reptiles and amphibians have remained scant since the pioneering work of Pregill et al. (1994). In addition, the impact of human populations on herpetological communities during Amerindian and colonial periods is sparsely documented although some works have attempted to tackle this question (Pregill, 1986; Steadman et al., 1984).

The recent exploration and excavation of fossil-bearing deposits in Guadeloupe and Marie-Galante considerably improve our knowledge of past Guadeloupean biodiversity (Grouard et al., 2014; Lenoble et al., 2009; Stouvenot et al., 2014). The present study focuses on reptile and amphibian remains collected from one of these sites, the Cadet 2 Cave, which lies on the southeastern coast of Marie-Galante, and documents the composition and evolution of the Marie-Galante herpetofauna over the past thirty thousand years.

Marie-Galante island and site description

Marie-Galante (61.223358 W; 15.893134 N) (Fig. 1) is a small, low-lying limestone island of approximately 158 km² (maximum altitude = 202 m). It probably emerged during the Late Calabrian about 800,000 years ago (Münch et al., 2013). Six squamate species occur nowadays on the island: three of them are considered to be native species (*Anolis ferreus*, *Sphaerodactylus fantasticus anidrotus* and *Thecadactylus rapicauda*) and three others as recently introduced species (*Iguana iguana*, *Gymnophthalmus underwoodi* and *Hemidactylus mabouia*). There are also three species of frogs, one native (*Eleutherodactylus martinicensis*) and two allochthonous (*Eleutherodactylus johnstonei* and *Scinax cf. x-signatus*). Several other currently extinct taxa have been mentioned by naturalists over the past centuries, including three squamates, the scincid *Capitellum mariagalantae* and two snakes (*Alsophis antillensis* and

Liophis juliae) (Breuil, 2002). In addition, the genus *Iguana* have been mentioned in Marie-Galante archaeological deposits dated from 200 to 1000 AD (Grouard, 2001). The Cadet 3 fossil deposit (Sierpe, 2011; Stouvenot et al., 2014) containing layers dated from 13,800 BC to modern time provides evidence of three additional extinct taxa, hitherto never mentioned on the island (*Boa* sp., *Ameiva* sp. and *Leiocephalus cuneus*). *Ameiva* was previously thought to have been present on Marie-Galante during the past by Breuil (2002), but clear evidence was lacking.

Cadet 2 is a flank margin cave (Lenoble et al., 2009) opening onto the cliff of the Capesterre terrace near the Cadet 3 site, about 250 m from the coast (Fig. 1). The site was first excavated by P. Courtaud from 2004 to 2007 in order to record Amerindian burials (Courtaud, 2011; Courtaud et al., 2005). Due to the paleontological potential of the site (Lenoble et al., 2009) another excavation was subsequently directed by S. Grouard in 2010 to investigate the pre-anthropogenic layers and to collect the vertebrate remains. This last excavation focused on two loci described below.

The first locus (Fig. 1) is located in the deepest part of the cave. It measures one square meter and reaches a depth of 1.4 meters. This locus contains a large part of the cave infilling. Above a basal accumulation of sands rich in seashells and land crab fragments (U5-D), the deposits correspond to a succession of bedded silt, divided into three subunits following the sedimentary structure (U5-C to U5-A). The organic silt fraction was radiocarbon dated at the *Centre de datation par le radiocarbone*, Lyon, (France). The dates range between 34,229–31,888 cal. B.C. and 11,909–11,530 cal. B.C. (Ref.: Ly 8496–8492) (Fig. 1). Above these levels, lies layer U4–U4', corresponding to an undated non-excavated archaeological level, probably of Holocene age. An archaeological pit was identified in layer U4 (ST 500 see Fig. 1). This structure is contemporaneous with the Amerindian occupation of the cavity, estimated to date from the 14th century AD (Courtaud, 2011; Courtaud et al., 2005).

The second locus was excavated over half a square meter and divided into six levels. The radiocarbon dating of a charcoal from level U5-b at the Erlangen laboratory (Germany) yielded ages of 28,413–27,425 cal. B.C. (Ref.: Erl 14,011). On the basis of the characteristics of the sediment facies, the stratigraphic units of this locus were correlated with layers U5-C and U5-B from the first locus, and are thus considered to be of Pleistocene age.

The whole assemblage is made up of 131,571 osteological remains, including 57,468 (48%) reptile and amphibian remains collected in all the layers except U5-D, which contained only few very fragmented bones.

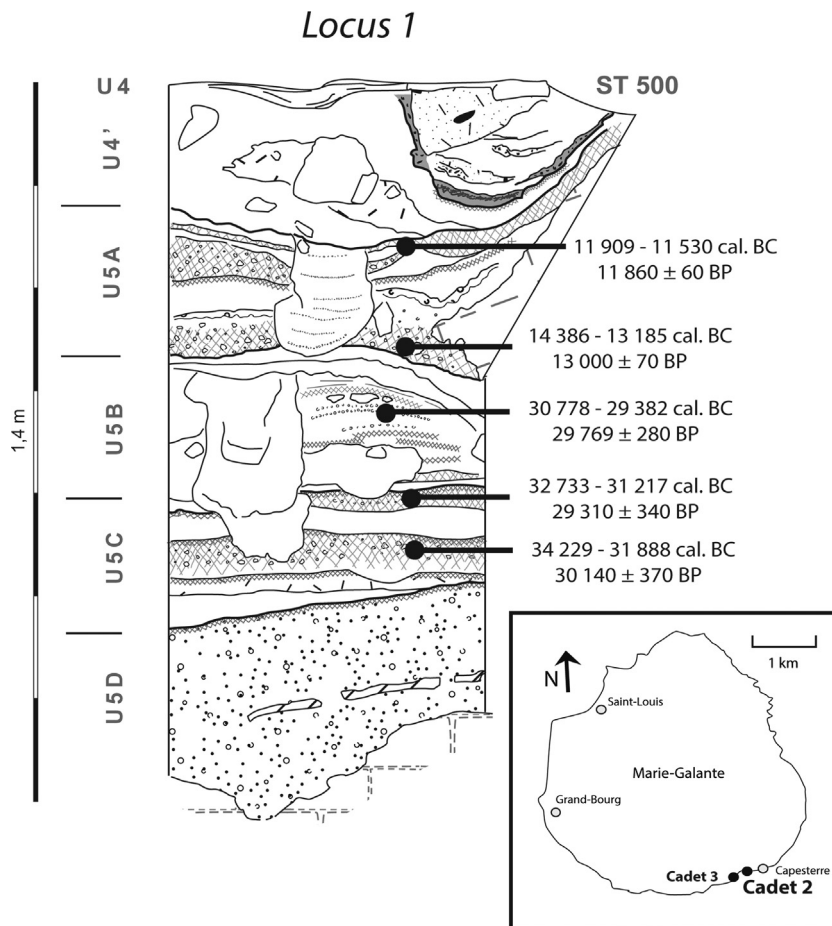


Fig. 1. Site location and stratigraphy of the first locus with radiocarbon dates.

Fig. 1. Localisation du site et stratigraphie du premier locus avec datations radiocarbone.

2. Material and methods

The sediment samples from the site were washed with water using a 0.5 mm sieve mesh. The osteological remains were collected with a binocular scope (Nikon SMZ1000).

The osteological collections used for the identification of the remains (see [Appendix 1](#)) come from the Muséum national d'Histoire naturelle (MNHN, Paris, France) (Comparative Anatomy—MNHN-ZA-AC—, Reptile and Amphibians—MNHN-RA—and UMR 7209 “Archéozoologie et archéobotanique” “Caribes”—MNHN-UMR7209—collections) and UMR 5199 CNRS “PACEA” (PACEA, Bordeaux, France). We also referred to several published osteological characteristics. In this study, we only describe the main osteological features used for the identification of each taxon.

The classifications employed here derive from several works concerning amphibians ([Frost et al., 2006](#); [Hedges et al., 2008](#)) and squamates ([Conrad, 2008](#); [Townsend et al., 2011](#)), including some on snakes ([Lee and Scanlon, 2002](#); [Vidal et al., 2010](#)).

The osteological features for frog identification are based on the synopsis by [Hedges et al. \(2008\)](#) and [Lynch \(1971\)](#).

The characteristics used to identify squamate cranial remains are those cited by [Conrad \(2008\)](#), [Estes et al. \(1988\)](#) and [Evans \(2008\)](#). Post-cranial identification is based on the works of [Etheridge \(1967\)](#), [Hoffstetter and Gasc \(1969\)](#) and [Lécuro \(1968, 1969\)](#). Several other works were used to specifically identify the Dactyloidae ([Etheridge, 1959](#); [Etheridge and De Queiroz, 1988](#); [Frost and Etheridge, 1989](#); [Nicholson et al., 2012](#); [Poe, 1998, 2004](#)), the Scincidae ([Greer, 1970](#); [Rao and Ramaswami, 1952](#)) and the Teiidae ([Kosma, 2004](#); [Pujos et al., 2009](#); [Tedesco et al., 1999](#)).

Snake vertebra identification is based on the works of [Albino and Carlini \(2008\)](#), [Albino \(2011\)](#), [Lee and Scanlon \(2002\)](#) and [Rage \(1984\)](#).

3. Results

Systematic account
Anura Duméril, 1806

Eleutherodactylidae Lutz, 1954

Eleutherodactylus sp. Duméril and Bibron, 1841–48,330 remains representing most anatomical parts. Minimal Number of Individuals (MNI) = 4,405 based on the ilia.

The eleutherodactylid frog attribution is based on the combined occurrence of the following features: elongated maxillary bearing a high number of teeth (t.), without lateral dermal ornamentation but with a thick maxillary shelf (M. s.) and short posterior process (M. p. pr) (Fig. 2A–B); fused sphenethmoids; unfused frontoparietals; fused prootic and frontoparietal; type 1 atlas articulation (*sensu* Lynch, 1971); atlas and second vertebra neural arches not fully ossified; sacral vertebra with distally weakly expanded and slightly posteriorly orientated sacral processes; elongated scapula with well individualized acromial and glenoid processes; ilium bearing a weak, medially incurved dorsal crest with a globular and laterally placed superior tuberosity and distally fused tibial and fibular. In addition, the occurrence of vomerine teeth is a feature encountered in the *Eleutherodactylus* genus (Hedges et al., 2008) (Fig. 2C).

These osteological features, combined with present geographical distribution data, allow us to attribute this frog to the genus *Eleutherodactylus*, and perhaps to a member of the *martincensis* series (*sensu* Hedges et al., 2008). The only extant members of this genus occur in the Lesser Antilles. These remains are present in all the Cadet 2 layers.

Squamata Oppel, 1811

Dactyloidae Fitzinger, 1843

Anolis cf. *ferreus* (Cope, 1864)–8638 remains corresponding to most skeletal parts. MNI = 215 based on the dentaries.

Many of the observed features point towards an attribution of these bones to an iguanid whereas others are typical of polychrotine iguanids (*sensu* Evans, 2008 = Dactyloidae *sensu* Townsend et al., 2011): maxillary bearing a triangular facial process forming an anterodorsal plate (ad. p.) grooved by a furrow (*canthus*) (c.) (Fig. 2D); fused frontals without dorsal keel or pineal foramen and medially fused ventral cranial crests (c. cr.) (Fig. 2E); parietal bearing a Y-shaped crest and a pineal foramen on its anterior margin; jugal of angular type morphology; no pterygoidian teeth. In addition, the blunt extremity of the dentary posterior process (p. pr.) (Fig. 2F) is characteristic of the *Anolis bimaculatus* series (Poe, 2004), which includes, among others, the North Lesser Antillean anoles. The maxillary and dentary tooth morphology is also characteristic of anoles; teeth are pleurodont and slightly labio-lingually flattened. The posterior teeth are tricuspid with a wider central cusp and two reduced anterior and posterior cusps. The anterior teeth tend to become more and more monocuspid.

The observed osteological features on all skeletal parts show that this taxon corresponds to one or more species of *Anolis* of the *bimaculatus* series (Poe, 2004). These remains are abundant in every Cadet 2 layer.

We estimated the fossil anole SVL size using the dental row length of each complete dentary by comparison with modern *A. ferreus* of known size. According to our estimations, fossil size ranges from 53 to 123 mm SVL, a range consistent with the present-day size of the Marie-Galante anole, *A. ferreus* (see Breuil, 2002). No significant size

differences emerge between the Pleistocene and Holocene Cadet 2 layers (Wilcoxon-Mann-Whitney test; P . val > 0.05) (Fig. 3A). In addition, the clearly bimodal distribution of fossil size corresponds perfectly to female (73 mm SVL maximum) and male (123 mm SVL maximum) *A. ferreus* sizes (Fig. 3B).

Sphaerodactylidae Underwood, 1954 cf. *Sphaerodactylus* sp. Wagler, 1830 – 1 femur. MNI = 1

This single femur has been identified on the basis of its morphological proximity with *S. fantasticus* and its reduced size (3 mm length), compared to all the other taxa described here. This taxon is only represented in the locus 2 Pleistocene layer.

Scincidae Gray, 1825

Mabuya (s. l.) sp. Fitzinger, 1826 (= cf. *Capitellum mariagalantae sensu* Hedges and Conn (2012)) – 2 maxillaries, 1 frontal, 2 parietals, 2 dentaries, 1 coronoid, 3 articular-surangulars, 10 dorsal vertebrae, 1 sacral vertebra, 5 caudal vertebrae, 3 pelvic girdles, 1 humerus, 3 femurs, 3 ulnas. MNI = 2

The following osteological characteristics allow us to identify this taxon as a Scincidae: maxillary bearing a bifid posterior process; fused frontals with weak intra-orbital constriction bearing slight ornamentation (or.) on its dorsal part and moderately strong, medially unconnected ventral cranial crests (c. cr.) (Fig. 4A–B); fused parietals bearing slight dermal ornamentation, a central pineal foramen, long posterior processes but shorter than the parietal table and a deep posteromedial notch; dentary with a straight ventral margin, well individualized posteroventral (pv. Pr.) and posterodorsal (pd. Pr.) processes and Meckel groove (M. g.) completely surrounded by bone on its anterior half (Fig. 4C–D); articular, prearticular (pa.) and surangular (sa.) fused and retroarticular process (ra. pr.) rounded, well-developed and slightly inclined medially (Fig. 4E); pleurodont, cylindrical and monocuspid teeth with rounded apex on maxillary and dentary bones.

In addition, the small size of these remains and their morphological similarity with *Mabuya* (*sensu lato*) lead us to attribute them to that genus, which is the only scincid genus traditionally recognized in the Lesser Antilles. Following Hedges and Conn (2012), *Mabuya sensu lato* is currently divided into sixteen genera but no osteological features have yet been proposed to differentiate them. Thus, relying exclusively on geographical criteria, we suggest an attribution to the Marie-Galante skink, *Capitellum mariagalantae sensu* Hedges and Conn (2012), (formerly *Mabuya mabuya*), mentioned for the last time by Dunn (1935). These fossil remains occur from the oldest to the youngest Cadet 2 layers but are absent from U5-B.

Teiidae Gray, 1829

Ameiva sp. (Meyer, 1795) – 2 premaxillaries, 8 maxillaries, 2 prefrontals, 4 frontals, 2 postorbitofrontals, 1 jugal, 2 pterygoids, 1 quadrate, 2 dentaries, 4 coronoids, 1 articular, 1 axis, 17 dorsal vertebrae, 3 second sacral vertebrae, 45 caudal vertebrae, 6 scapulocoracoids, 1 ischium, 3 humeri, 1 tibia and 2 femurs. MNI = 4

The main elements clearly show teiid squamate features: maxillary with long and high facial process (f. p.) and without dermal ornamentation (Fig. 4F); fused

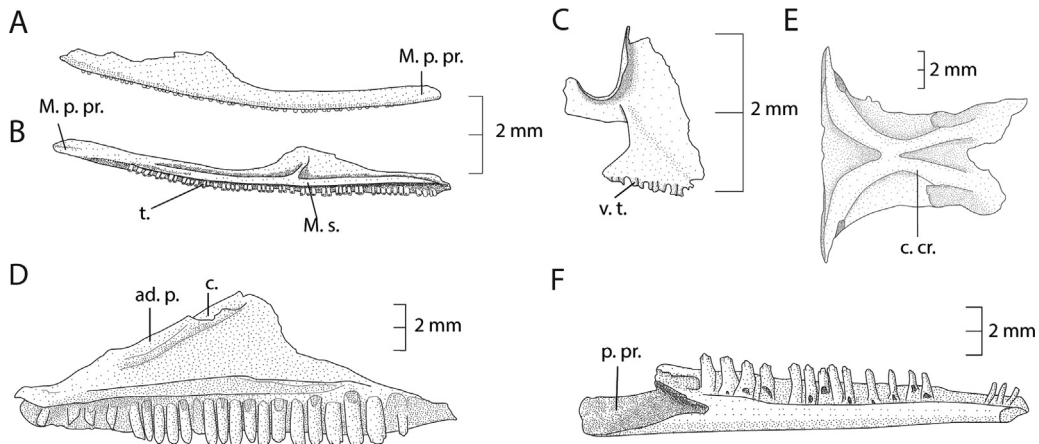


Fig. 2. *Eleutherodactylus* sp. A and B. Maxillary, labial and lingual views. C. Vomer, dorsal view. *Anolis cf. ferreus*. D. Maxillary, lingual view. E. Frontal, ventral view. F. Dentary, lingual view.

Fig. 2. *Eleutherodactylus* sp. A et B. Maxillaire, vue labiale et linguale. C. Vomer, vue dorsale. *Anolis cf. ferreus*. D. Maxillaire, vue linguale. E. Frontal, vue ventrale. F. Dentaire, vue linguale.

frontals with deep dorsolateral nasal bone impressions (N. i.), a clearly visible dorsal ornamentation (or.) and low ventral cranial crests (c. cr.) without anteroventral descendant process (Fig. 4G–H); dentary Meckel groove (M. g.) fully open and incurved dentary ventral margin (Fig. 4I); articular angular process ventrally orientated; pleurodont bicuspid or monocuspid teeth surrounded at their bases by dental cement and basally pierced by a subcircular replacement pit; procoelous vertebrae with well-developed zygosphenes that lack an anterior notch. In addition, the absence of pterygoidian teeth and the Meckel groove opening only visible in lingual view are characteristic of *Ameiva* and the occurrence of monocuspid posterior teeth with a rounded apex is a feature occurring in the Lesser Antillean *Ameiva* taxa (*A. fuscata*, *A. griswoldi*, *A. plei* and *A. pluvianotata*) (Kosma, 2004; Pregill, 1984).

These features allow us to identify this taxon as a member of the genus *Ameiva*, possibly comprised in the Lesser Antillean *Ameiva* clade on the basis of its dental

morphology. We estimate the size of this squamate at around 150–200 mm SVL, which is similar to *A. cineracea* (from Basse-Terre), but smaller than *A. major* (from Petite-Terre), the two previously described Guadeloupean ameivas considered to have become extinct recently (Breuil, 2002) in Guadeloupe islands. A comparison with these taxa is impossible as their skeletal morphology remains unknown. The ameiva remains are present from the oldest to the youngest Cadet 2 layers but are absent from U5–B.

Serpentes Linnaeus, 1758

Scolecophidia Cope, 1864

Cf. *Antilotyphlops* Richmond, 1966–169 dorsal and caudal vertebrae.

These vertebrae (Fig. 5A–B) bear typical scolecophid-ian features. They are small with a centrum length ranging from 0.9 to 1.65 mm. They bear a zygosphenes/zygantrum articulation (zs.) but neither neural spine nor hemal keel. The neural arch posterior margin is weakly notched. The prezygapophyseal processes (pz. pr.) are long, slender and

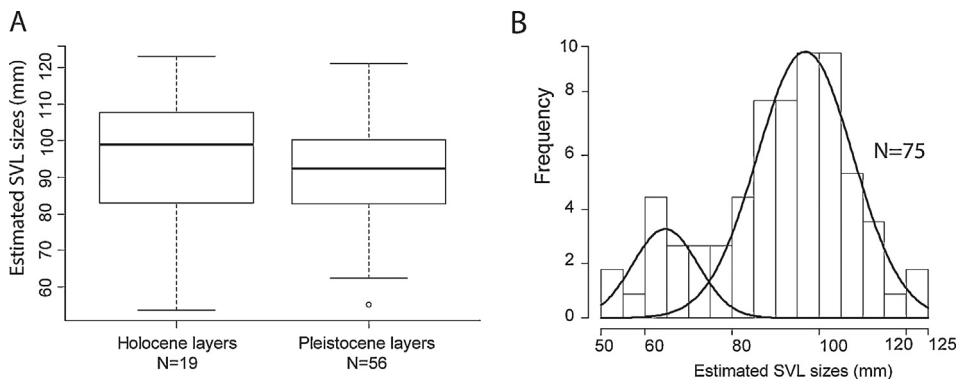


Fig. 3. A. Distribution of the Snout-Ventral length (SVL) estimated from the dentaries dental length of *Anolis cf. ferreus* in the Holocene and Pleistocene Cadet 2 layers. B. Histogram containing all the estimated SVL of the fossils and Gaussian distributions resulting of a Gaussian mixture analysis.

Fig. 3. A. Distribution des longueurs museau-cloaque (SVL) estimées à partir des longueurs des rangées dentaires d'*Anolis cf. ferreus* dans les niveaux d'âge Holocène et Pléistocène de Cadet 2. B. Histogramme de toutes les tailles estimées sur les fossiles et distributions gaussiennes résultants d'une analyse de mélanges gaussiens.

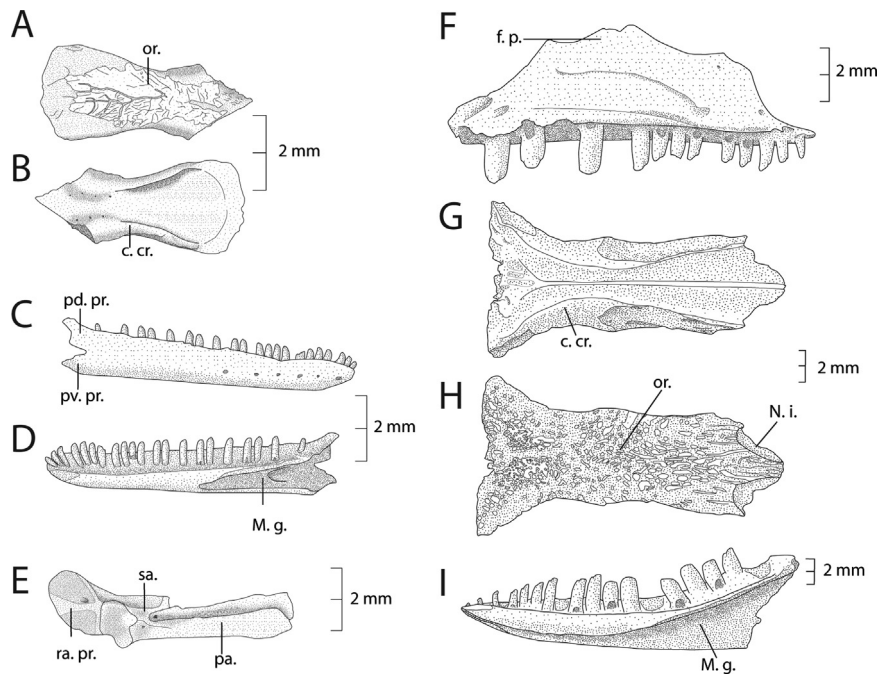


Fig. 4. Cf. *Capitellum mariagalantae*. A and B. Frontal, dorsal and ventral views. C and D. Dentary, labial and lingual views. E. Articular-prearticular, dorsal view. *Ameiva* sp. F. Maxillary, lingual view. G and H. Frontal, ventral and dorsal views. I. Dentary, lingual view.

Fig. 4. Cf. *Capitellum mariagalantae*. A et B. Frontal, vues dorsale et ventrale. C et D. Dentaire, vues labiale et linguale. E. Articulaire-préarticulaire, vue dorsale. *Ameiva* sp. F. Maxillaire, vue linguale. G et H. Frontal, vues ventrale et dorsale. I. Dentaire, vue linguale.

anteriorly oriented. The cotyle is dorsoventrally flattened and there are no paracotylar foramina. Synapophyses are simple and rounded.

According to these features, these bone remains can be attributed to a scolecophidian snake. They could be related to a member of the *Antillotyphlops* genus, the only genus occurring today in the North of the Lesser Antilles (Hedges et al., 2014). These typical vertebrae occur from Pleistocene to Holocene Cadet 2 layers but are absent from U5-C and U5-B.

Alethinophidia Nopcsa, 1923

Boidae Gray, 1825

Boa sp. Linnaeus, 1758–16 dorsal vertebrae.

These vertebrae (Fig. 5C–E) bear all the *Boa* features: they are strongly built, are wider than they are long and have a high neural arch and neural spine (ns.). The neural arch posterior margin is strongly notched, the prezygapophyseal facets (prz. f.) are long and laterally oriented and the prezygapophyseal processes (pz. pr.) are present but short. The zygosphene (zs.) is thick from an anterior view and its anterior margin is more or less concave from a dorsal view. From a ventral view, there is a strong precondylar constriction and the hemal keel (h. k.) is thin with a blunt ventral margin. A paracotylar foramen (p. f.) is present on each cotyle side.

These features allow us to attribute these vertebrae to a member of the genus *Boa*. The small size of the vertebrae (centrum length ranging from 2.8 to 4.2 mm) suggests very small specimens with a SVL size of around 80 cm. This raises the question of the juvenile character of these vertebrae, a hypothesis also supported by the fact that vertebral cotyles

and condyles are wider than high (Albino, 2011). Another possibility could be membership in a dwarf species, but the material is too sparse to provide a clear answer to this question. This taxon is only present in the Pleistocene U5-C and Locus 2 layers of Cadet 2.

Colubroidea Oppel, 1811

Cf. *Alsophis* sp. Fitzinger, 1843 - 155 dorsal and caudal vertebrae.

These vertebrae (Fig. 5F–H) are weakly built and are relatively more elongated than those of non-colubroid Cadet 2 snakes. The centrum is longer than wide and has length ranges from 0.8 to 3.5 mm. In dorsal view, the zygosphene (zs.) anterior margin is slightly lobed. The neural spine (n. s.) is longer than it is high. The synapophysis (sy.) is well individualized with a diapophysis slightly bigger than the parapophysis. The prezygapophyseal processes (pz. pr.) are conical, thick, blunt, laterally oriented and their lengths correspond to half of the prezygapophyseal facet (prz. f.) length. Paracotylar foramina (p. f.) are present on each side of the condyle. From a lateral view, the hemal keel (h. k.) is well marked.

On the basis of these features, these vertebrae can be ascribed to a colubroid snake. In addition, the prezygapophysis morphology, thicker and more laterally oriented than those of the other Cadet 2 colubroid vertebrae, allows us to advocate their attribution to the genus *Alsophis*. These vertebrae occur in all the Cadet 2 layers.

Colubroidea sp. 1–13 dorsal vertebrae.

These vertebrae (Fig. 5I) are similar to those previously described for cf. *Alsophis* sp., except that they are smaller (maximal centrum length = 1.2 mm) and they bear

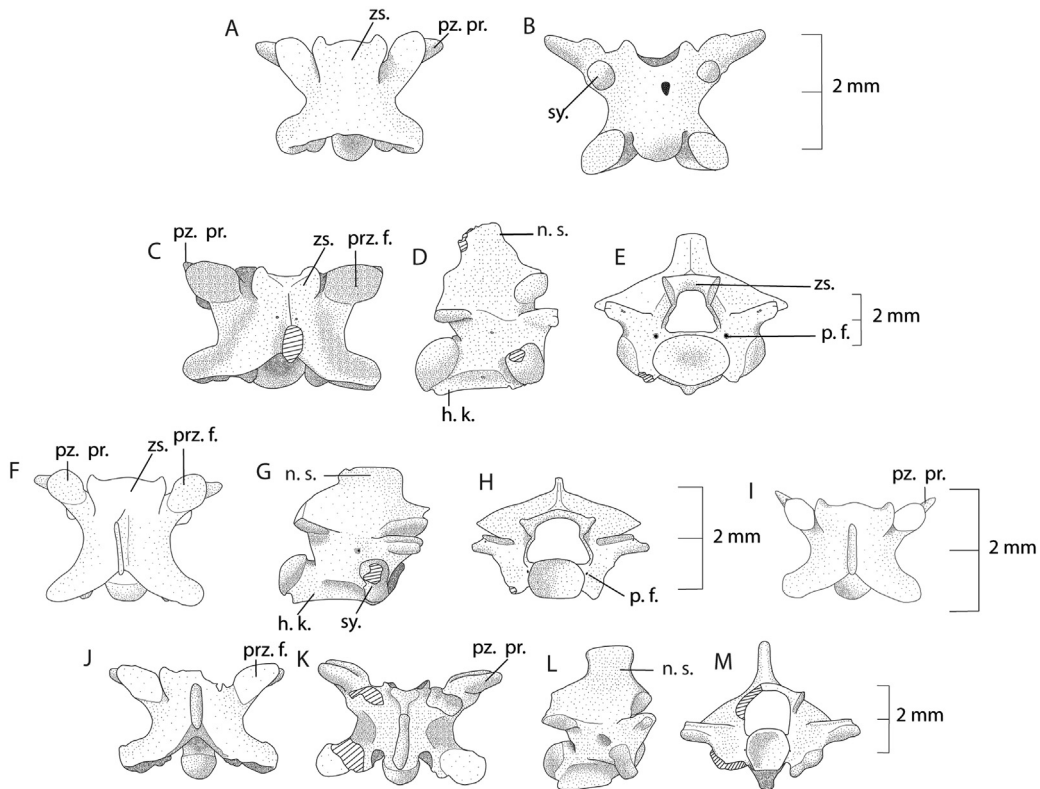


Fig. 5. Cf. *Antillotyphlops*. A–B. Dorsal vertebra, dorsal and ventral views; *Boa* sp. C–E. Dorsal vertebra, dorsal, lateral and anterior views. Cf. *Alsophis* sp. F–H. Dorsal vertebra, dorsal lateral and anterior views. Colubroidea sp. 1. I. Dorsal vertebra, dorsal view. Colubroidea sp. 2. J–M. Dorsal vertebra, dorsal, ventral, lateral and anterior views.

Fig. 5. Cf. *Antillotyphlops*. A et B. Vertèbre dorsale, vues dorsale et ventrale; *Boa* sp. C–E. Vertèbre dorsale, vues dorsale, latérale et antérieure. Cf. *Alsophis* sp. F–H. Vertèbre dorsale, vues dorsale, latérale et antérieure. Colubroidea sp. 1. I. Vertèbre dorsale, vue dorsale. Colubroidea sp. 2. J–M. Vertèbre dorsale, vues dorsale, ventrale, latérale et antérieure.

longer, sharper and anteriorly oriented prezygapophyseal processes (pz. pr.).

These vertebrae could possibly belong to a member of the genus *Liophis* (possibly *Erythrolamprus* following Curcio et al., 2009), which is with *Alsophis* the only genus of colubroid snake ever observed on Marie-Galante (Breuil, 2002), but the vertebral morphology of the latter is still undescribed and remains unknown to us for the time being. These vertebrae occur in all the Cadet 2 layers.

Colubroidea sp. 2–1 dorsal vertebra.

This vertebra (Fig. 5J–M) is similar to those previously described for cf. *Alsophis* but it presents some significant differences. It bears a more marked neural arch median constriction than the other vertebrae in dorsal view. The neural spine (n. s.) is also different; it is high and thin with anterior and posterior borders slightly overhanging. The prezygapophyseal processes (pz. pr.) are shorter and thicker and the prezygapophyseal articular facets (prz. f.) have a more elongated shape.

For the time being, we cannot suggest a specific attribution for this vertebra. It could be from an unknown taxon from the island fauna. This single vertebra was recovered in the Locus 2 Pleistocene layer.

4. Discussion

We identified at least ten taxa in the different sampled layers of Cadet 2, all of which occur in the Pleistocene layers, which are currently the oldest known Marie-Galante fossil levels. Consequently, our study provides the first information on Marie-Galante Pleistocene fauna prior to 14,000 B.C. (Stouvenot et al., 2014).

Three taxa are only present in the Pleistocene layers at Cadet 2: *Boa* sp., Colubroidea sp. 2 and cf. *Sphaerodactylus* sp. *Boa* sp. was previously reported at Cadet 3 (Stouvenot et al., 2014), where, like at Cadet 2, this taxon only occurs in Pleistocene levels. Colubroidea sp. 2 had not been identified up until now but this attribution will require further investigation. *Sphaerodactylus* is a very small sphaerodactylid gecko still occurring on Marie-Galante (Breuil, 2002; Powell and Henderson, 2012). This is the first fossil record of this taxon on the island and it shows that it was already present there during the Late Pleistocene. This is not surprising given the existence of a Marie-Galante endemic sub-species (*Sphaerodactylus fantasticus adrinotus*) (see Breuil, 2002), which was the first evidence of its local evolution on the island.

Site	Cadet 2	Cadet 2	Cadet 2	Cadet 3	Cadet 2	Cadet 3	Cadet 2	Cadet 3	Cadet 3	Cadet 3	Cadet 2	Cadet 3			
Layer	U5C	U5B	Locus 2	K	U5A	J	U4	I	G-H	D-E-F	ST500	A-B-C			
Age	~32 000 BC	~30 000 BC	~28 000 BC	~13 800 BC	~12 000 BP	13 800 BC - 2 750 BC	Holocene	13 800 BC - 2 750 BC	2 750 BC - 1 300 BC	1 300 BC - 1 000 AD	~1300 AD	Modern <1000AD	Historically mentioned (17 th -20 th centuries)	Nowadays present	
<i>Scinax x-signatus</i>															X
<i>Eleutherodactylus</i> sp.	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
<i>Iguana</i> sp.															X
<i>Hemidactylus mabouia</i>															X
<i>Gymnophthalmus underwoodi</i>															X
<i>Thecadactylus</i> sp.															X
<i>Leiocephalus</i> sp.															X
<i>Anolis ferreus</i>	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
<i>Sphaerodactylus fantasticus</i>			X												X
cf. <i>Antillotyphlops</i>			X	X	X	X	X	X	X	X	X	X	X	X	X
cf. <i>Alsophis</i>	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Colubridae sp 1 or cf. <i>Liophis</i>	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
<i>Capitellum mariagalantae</i>	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
<i>Ameiva</i> sp.	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
<i>Boa</i>	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Colubroidae sp. 2			X												X

Fig. 6. Table containing the distribution of the taxa in the Cadet 2 and 3 (Sierpe, 2011; Stouvenot et al., 2014) layers along with their historical mentions (see Breuil, 2002), present occurrence (Powell and Henderson, 2012) and minimal period of occurrence on Marie-Galante (in grey).

Fig. 6. Tableau de distribution des taxons dans les niveaux de Cadet 2 et 3 (Sierpe, 2011; Stouvenot et al., 2014) avec leurs mentions historiques (voir Breuil, 2002), leur présence actuelle (Powell et Henderson, 2012) et leur période minimale de présence à Marie-Galante (en gris).

The other identified taxa have been previously observed alive on the island and occur in all the Cadet 2 layers. This is the case for the *Eleutherodactylus* frogs, currently represented on the island by two species: *E. marticensis* and *E. johnstonei* (Breuil, 2002; Powell and Henderson, 2012). The Marie-Galante skink (cf. *Capitellum mariagalantae*) was observed on the island for the last time in 1830 and is since considered to be extinct (Hedges and Conn, 2012). This taxon is also present in the Cadet 3 site (Stouvenot et al., 2014). Ameivas were reported for the last time in the 17th century (see Breuil, 2002). This taxon is also present in several other Marie-Galante sites (Grouard, 2001, 2003; Stouvenot et al., 2014). Anoles (*Anolis* cf. *ferreus*) are still widely present on the island (Breuil, 2002) and fossil anole remains have already been mentioned at other sites (Grouard, 2001, 2003; Stouvenot et al., 2014). As for the snakes, *Antillotyphlops* is considered to have become extinct very recently on Marie-Galante (Breuil, 2002), *Alsophis* disappeared from Marie-Galante during the 20th century (Breuil, 2002) and *Liophis* (Colubroidea sp. 1?) even earlier at the end of the 19th century (Henderson, 1992). Bones from these three snakes were also reported at Cadet 3 (Stouvenot et al., 2014).

Evolution of the species composition

Our data shed light on the herpetological biodiversity stability during the Pleistocene and Holocene periods (Fig. 6). Accordingly, only two taxa (*Boa* sp. and Colubroidea sp. 2) seem to have disappeared between Pleistocene and Holocene periods. At the present time, this fact is difficult to explain due to the lack of Pleistocene environmental data for the island. The case of the boa, still represented in the Lesser Antilles on Dominica (*Boa nebulosa*) and Saint Lucia (*B. orophias*) by endemic taxa, is very interesting but the study of larger series is indispensable to enhance our knowledge of the taxonomic status, biological features and extinction causes of this snake.

This apparent stability no longer subsists for the extant island fauna. Among the seven taxa that appear to be present since the Late Pleistocene in Cadet 2, only three of them still occur on the island today (*Eleutherodactylus* sp., cf. *Sphaerodactylus* sp. and *Anolis* cf. *ferreus*). Ameivas, skinks and all the snakes are now extinct. This fact,

combined with the occurrence of these taxa in the most recent Cadet 2 layers, in the Late Holocene Cadet 3 layers (Stouvenot et al., 2014) and historical mentions of these taxa (see Breuil, 2002) shows that these extinctions occurred during the last few centuries, after European colonization. Many explanations can be advanced to account for these extinctions, which are widespread in all anthropized insular systems. In the Lesser Antilles, they are generally explained by the introduction of new predators such as the mongoose (*Herpestes javanicus*), which was introduced by man in order to eradicate rats and venomous snakes (Henderson, 1992, 2004; Lorvelec et al., 2004), but this probably just represents one factor among others, such as habitat destruction or the introduction of new competitors.

However, all taxa were not impacted in the same way and the first data concerning fossil anole size shows that the size of this taxon has remained the same from the Late Pleistocene until the present, for a period of more than 30,000 years. Our data do not seem to comply with the taxon cycle theory and the supposed classical existence of a second anole species on the island (Roughgarden, 1995). This also shows that *A. ferreus*, still common on the island today, seems to display greater resilience to human impact than most of the other currently extinct squamate taxa. Unlike other local squamates, this anole is mostly arboreal and this trait may have protected it from terrestrial allochthonous predators. However, this explanation alone is not necessarily the only cause for the persistence of this taxon and the observed patterns of extinction may also be explained with multifactorial models.

Conversely, some frog and squamate taxa that do not occur in Cadet 2 are now present on the island. Predictably, some of them are commonly recognized as recently introduced taxa: *Scinax* cf. *x-signatus*, *H. mabouia*, and *Gymnophthalmus underwoodi*, but some of the others were previously thought to be natives or of uncertain status. The Turnip-tailed gecko (*T. rapicauda*), for instance, is absent from Cadet 2 and only occurs in a Cadet 3 layer dated to around 1000 AD (Stouvenot et al., 2014). The absence of earlier fossil remains of this species could be further evidence of its recent arrival on the island. Another interesting

case is the absence of iguanas in the fossiliferous localities while this taxon is present in pre-Columbian archaeological deposits (Bochaton, com. pers.; Grouard, 2001, 2003, 2007, 2010), a fact that could also be related to their recent arrival. The Curly-tailed lizard (*Leiocephalus cf. cuneus*) is also absent from Cadet 2, but present in Cadet 3 in deposits possibly contemporaneous with a pre-Columbian occupation layer and now extinct on the island. In the same way as the iguana, the absence of this species in Cadet 2 is hard to explain and both taxa may possibly have been introduced on the island by human populations. An overview of all the fossil and subfossil herpetological data is still in progress in order to test these hypotheses and to clearly define the colonization scenario for each taxon in Marie-Galante, and more generally in the Guadeloupe islands.

5. Conclusion

Only three out of the ten indigenous reptile and amphibian taxa occurring in the Pleistocene layers of Cadet 2 on Marie-Galante are still extant on the island (*Anolis cf. ferreus*, *S. fantasticus* and *Eleutherodactylus* sp.), which points to an extinction rate of at least 70%. Among those extinctions, only two (*Boa* sp. and Colubroidae sp. 2) are probably anterior to the human occupation of the island because they only occur in Pleistocene layers. But most of the herpetofauna, which remained stable for more than 30,000 years, was eliminated and replaced during the past two or three centuries. The Marie-Galante herpetofauna seems to be a demonstration of what is generally called the present sixth mass extinction crisis (Barnosky et al., 2011). This massive extinction is directly linked to human impact on the biosphere. Our approach also confirms the importance of integrating fossil and subfossil data to enhance our comprehension of the dynamics of herpetological communities after anthropization.

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Appendix 1. Comparative specimens used

Ameiva cf. bifrontata (MNHN-UMR 7209-343); *Ameiva chrysolema* (MNHN-ZA-AC 1944-74); *Ameiva plei* (MNHN-RA 1991.4275; MNHN-UMR 7209-405); *Ameiva surinamensis* (MNHN-RA 1991.4034); *Ameiva undulata* (MNHN-RA 1991.4276); *Anolis desiradei* (UMR-5199 201111-A; UMR-5199 221111-A; UMR-5199 231111-A; UMR-5199 250311-A; UMR-5199 251111-A); *Anolis ferreus*

(UMR-5199 071111-A; UMR-5199 161111-A; UMR-5199 161112-B; UMR-5199 181112-A; MNHN-UMR 7209-655; MNHN-UMR 7209-656; MNHN-UMR 7209-674; MNHN-UMR 7209-675; MNHN-UMR 7209-676; MNHN-UMR 7209-677; MNHN-UMR 7209-678; MNHN-UMR 7209-679; MNHN-UMR 7209-680; MNHN-UMR 7209-681; MNHN-UMR 7209-682; MNHN-UMR 7209-683; MNHN-UMR 7209-684; MNHN-UMR 7209-692); *Anolis marmoratus* (MNHN-UMR 7209-41; MNHN-UMR 7209-238; MNHN-UMR 7209-239; MNHN-UMR 7209-240; MNHN-UMR 7209-242; MNHN-UMR 7209-243; MNHN-UMR 7209-245; MNHN-UMR 7209-246; MNHN-UMR 7209-247; MNHN-UMR 7209-248); *Anolis pogus* (MNHN-UMR 7209-687; MNHN-UMR 7209-688; MNHN-UMR 7209-689); *Anolis roquei* (MNHN-UMR 7209-372; MNHN-UMR 7209-404a; MNHN-UMR 7209-404b; MNHN-UMR 7209-686); *Hemidactylus mabouia* (MNHN-UMR 7209-409; MNHN-UMR 7209-697); *Leiocephalus carinatus* (MNHN-UMR 7209-685); *Mabuya multifasciata* (MNHN-ZA-AC 1942-52); *Sphaerodactylus macrolepis* (MNHN-UMR 7209-696; MNHN-UMR 7209-697); *Thecadactylus oskrobapreinorum* (MNHN-UMR 7209-693); *Thecadactylus rapicauda* (UMR-5199 160312-A).

Alsophis antillensis (MNHN-UMR 7209-17); *Alsophis rijgersmaei* (MNHN-UMR 7209-406); *Boa constrictor constrictor* (MNHN-ZA-AC 1876-250; MNHN-UMR 7209-335; MNHN-UMR 7209-672).

Eleutherodactylus johnstonei (MNHN-UMR 7209-53; MNHN-UMR 7209-403a; MNHN-UMR 7209-403b; MNHN-UMR 7209-403c; MNHN-UMR 7209-403d; MNHN-UMR 7209-403e; MNHN-UMR 7209-403f; MNHN-UMR 7209-403g; MNHN-UMR 7209-403h; MNHN-UMR 7209-407); *Eleutherodactylus martinicensis* (MNHN-UMR 7209-410; MNHN-UMR 7209-671).

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