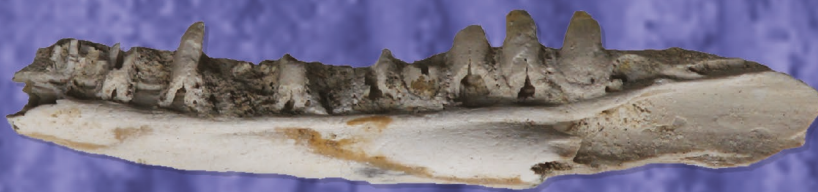


**Taphonomic analysis of a Caribbean
subfossil herpetofaunal bone assemblage
(Marie Galante Island, Lesser Antilles)**

Morgane SAYAH, Arnaud LENOBLE & Corentin BOCHATON



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Taphonomic analysis of a Caribbean subfossil herpetofaunal bone assemblage (Marie Galante Island, Lesser Antilles)

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ABSTRACT

Taphonomic analyses are of primary importance to understand the accumulation processes of fossil vertebrate bone assemblages. These approaches are fundamental in archaeological contexts in which the role of humans in the formation of an accumulation must be investigated in detail. However, taphonomic works have so far focused on temperate regions and mammals and few studies extensively deal with other vertebrates, especially the herpetofauna, and tropical areas. This results in an important gap in the scientific literature, which has a strong impact on the paleoecological and zooarchaeological research in the areas where squamates and amphibians are well-represented. In this paper, we present a detailed taphonomic study of a large herpetofaunal assemblage of nearly 11 000 bones collected in the Abri Cadet 3, on Marie Galante Island, and dated from the beginning of the Holocene to the Amerindian period. Obtained results don't support the role of humans in the constitution of the assemblage despite the occurrence of clear archaeological layers in the site. The most-likely culprit for the creation of the bone assemblage is a small nocturnal raptor (i.e., *Athene cunicularia guadeloupensis* (Ridgway, 1874) or *Tyto insularis* (Pelzeln, 1872)). We also conduct a comparison with the other available deposits from Marie Galante, highlighting the diversity of accumulation processes in the different nearby cave sites but also the lack of detailed taphonomic studies which would be needed to explain this diversity.

KEY WORDS

Amphibians,
squamates,
paleoecology,
predation,
taphonomy,
West Indies.

RÉSUMÉ

Analyse taphonomique d'un assemblage d'ossements subfossiles d'herpétofaune caribéenne (île de Marie-Galante, Petites Antilles).

Les analyses taphonomiques sont indispensables à la compréhension des processus d'accumulation des assemblages fossiles d'ossements de vertébrés. Ces approches sont fondamentales dans les contextes archéologiques, où le rôle des humains dans la constitution de l'assemblage doit être étudié en détail. Cependant, les études taphonomiques se sont jusqu'à présent concentrées sur les régions tempérées et les restes de mammifères et peu d'études concernent les autres groupes de vertébrés, notamment l'herpétofaune, ainsi que les aires tropicales. Cela résulte en un important biais dans la littérature scientifique qui impacte fortement les études paléoécologiques et archéozoologiques dans les aires géographiques où les squamates et amphibiens sont bien représentés. Dans cet article, nous présentons une analyse taphonomique de près de 11 000 ossements d'herpétofaune collectés dans l'abri Cadet 3 sur l'île de Marie-Galante et datés entre le début de l'Holocène et la période amérindienne. Les résultats obtenus ne supportent pas l'hypothèse du rôle des populations humaines dans la constitution de l'assemblage, malgré la présence de niveaux stratigraphiques archéologiques bien caractérisés dans le site. L'agent accumulateur le plus probable est un petit rapace nocturne (i.e., *Athene cunicularia guadeloupensis* (Ridgway, 1874) ou *Tyto insularis* (Pelzeln, 1872)). Nous effectuons également une comparaison avec les autres sites fossiles de Marie-Galante et mettons en évidence la diversité des modes d'accumulations dans les différentes grottes voisines de Cadet 3, mais également le manque d'études taphonomiques détaillées qui seraient nécessaires pour pouvoir interpréter ces différences.

MOTS CLÉS

Amphibiens,
squamates,
paléoécologie,
prédation,
taphonomie,
Caraïbes.

INTRODUCTION

Taphonomic studies play a crucial role in understanding the processes of bone accumulation in both paleontological and archaeological contexts (Lyman 1994). They provide insights into the composition bias of fossil assemblages compared to natural communities, which is essential for assessing the paleobiodiversity and past environments (Terry 2010; Zeitoun *et al.* 2019). Taphonomy also plays a significant role in investigating human behaviors, such as hunting (Piper & Rabett 2009) and practices like funerary and cannibalistic behaviors (Andrews & Fernández-Jalvo 2003). Additionally, it sheds light on the behaviors of non-human species extinct taxa such as raptors and carnivorans (Marean & Ehrhardt 1995). However, taphonomic research has primarily focused on the northern hemisphere, although some studies have started to address this bias (i.e., Montalvo *et al.* 2008; Hawkins *et al.* 2019). Previous works also concentrate on mammal bone accumulations. This research bias has two significant implications. Firstly, it compromises the accuracy and relevance of paleoecological and zooarchaeological studies conducted in most regions worldwide. Secondly, even when taphonomic studies are conducted on fossil material, the lack of modern and fossil comparative samples makes challenging to interpret the results. Squamates and amphibians (Bailon 2011), which are abundant in tropical areas and among the most neglected geographic regions, are particularly understudied in this regard.

The insular Caribbean area, despite its richness in squamates and amphibian taxa (Henderson & Powell 2009), which are frequently found in paleontological and archaeological deposits (Olson *et al.* 1982; Pregill *et al.* 1994; Bochaton 2022), is no exception. In this respect, most paleontological studies dealing with bone remains collected in natural deposits are conducted

without clear evidence allowing for the identification of the accumulation mode and, consequently, the significance of the assemblage in terms of past biodiversity (Pregill *et al.* 1988; Steadman *et al.* 2015; Kemp & Hadly 2016). This issue is critical as it hinders the construction of hypotheses about species that may be absent from the deposits. Furthermore, it renders any assumptions regarding the composition of past animal communities irrelevant, as the filter between the natural and fossil communities remains unknown. Therefore, combining different types of deposits with potentially distinct accumulation modes (e.g. natural and archaeological deposits) remains the best approach to obtain a representative image of past biodiversity, particularly in well documented islands such as the Guadeloupe archipelago (Bochaton *et al.* 2021b). In an attempt to address these issues, some recent taphonomic studies have been conducted on modern bone accumulations in Dominica to establish a comparative framework for the study of Caribbean fossil assemblages (Stoetzel *et al.* 2016a, 2021). However, no comprehensive taphonomic study of Caribbean herpetofaunal fossil assemblages has been undertaken to date.

In this paper, we aim to fill this gap by conducting an in-depth taphonomic analysis of the herpetofaunal fossil assemblage collected from Abri Cadet 3 on Marie Galante Island (Stouvenot *et al.* 2014). Several squamate and amphibian archaeological assemblages from this island have been subject to taphonomic investigations as part of zooarchaeological studies (Bochaton *et al.* 2016, 2019a, b). However, despite preliminary taphonomic observations of the herpetofaunal components in several natural bone accumulations in caves on Marie Galante (e.g. grotte Blanchard: Bailon *et al.* 2015; grotte Cadet 2: Bochaton *et al.* 2015), no thorough analysis has been conducted in this specific depositional environment. This lack of investigation is particularly problematic in the case

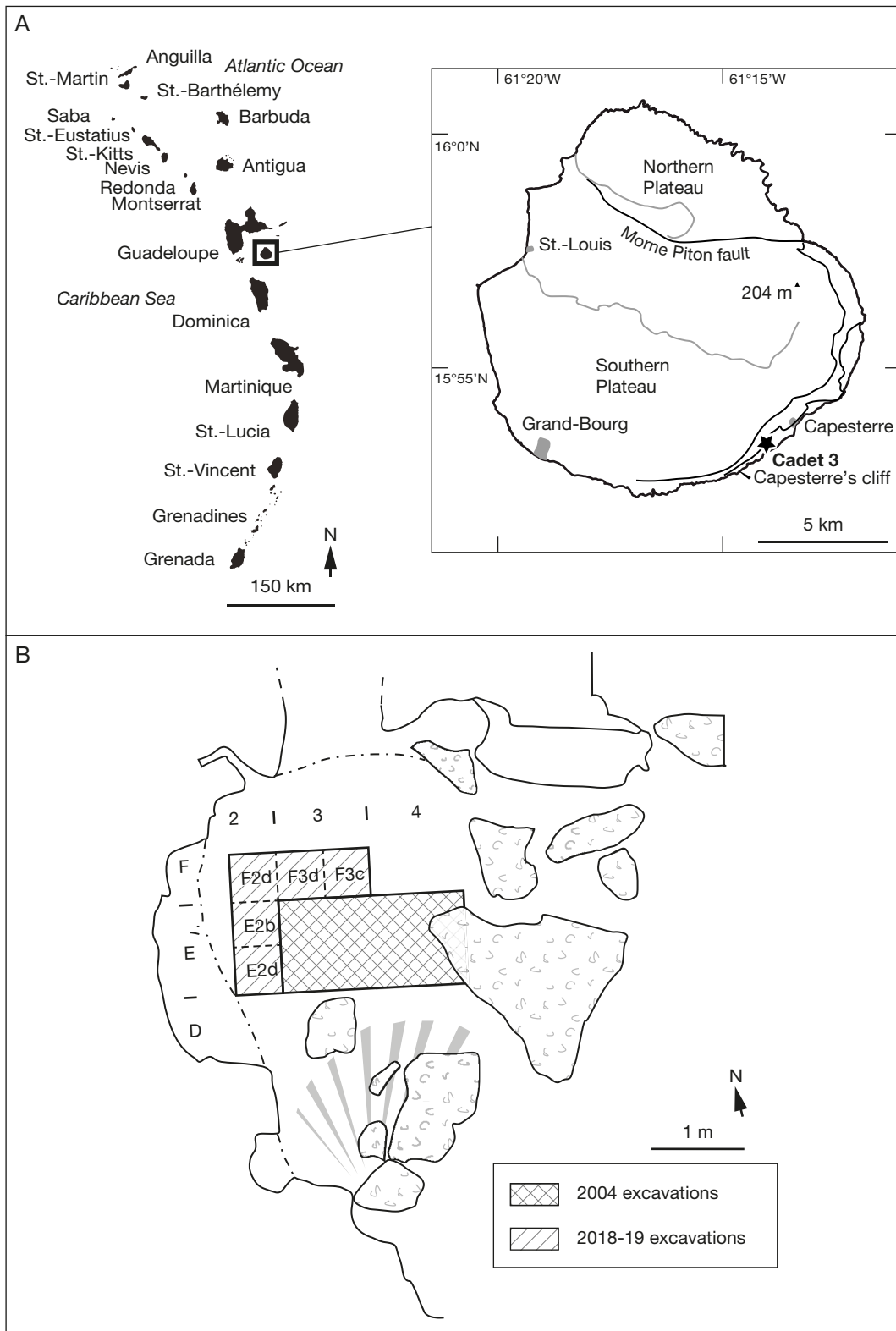


FIG. 1. — **A**, Location of Marie Galante Island in the Lesser Antilles and of the Cadet 3 (asterisk) site on Marie Galante; **B**, plan of the 2018/2019 excavation showing the location of the studied faunal sample (square F3c).

of Abri Cadet 3, which has layers indicating human occupation (Stouvenot *et al.* 2014), raising the possibility that some of the numerous micro-faunal remains in the sediment might reflect anthropic behaviors. Therefore, we chose to conduct

a taphonomic investigation of the herpetofaunal material, representing the majority of the bone assemblage, to explore the potential roles of human activities and/or natural accumulator agents in the formation of the bone accumulation.

TABLE 1. — Lithostratigraphy of the Abri Cadet 3.

Member	Layer	2004 units	Description	Formation process
Upper	1	A	–	Trampling
	2	B-D	Loose grey-brown to brown silty sand, containing sub-centimetric calcareous granules and supra-decimetric lenses of ashy sediment or charcoal	Runoff
Median	3	F-H	Matrix-supported brown to light grey loose silt, rich in granules, small calcareous pebbles, crab and gastropod shells, including lenses of poorly sorted pebbles.	Debris flow & runoff
	4	I	Dark grey to brown silt with fine sands	Paleosol
Lower	5	J	Massive cream-colored silt slightly indurated	Alteration (decarbonization + phosphatization)
	6	K	Massive reddish-brown to yellowish-brown calcareous sandy silt, rich in vertebrate bones	Runoff deposit

We will then compare these results with data from other deposits on Marie Galante and discuss the importance of identifying the accumulator agent more precisely for understanding the well-documented past biodiversity of the island.

THE SITE OF CADET 3

Cadet 3 is a rock shelter located on the southern coast of Marie Galante Island in the Guadeloupe archipelago (Fig. 1A). This rock shelter is approximately 6 m wide, with a depth and height of 4 m. It is situated a few meters above sea level and 250 m away from the seashore. The site is immediately adjacent to grotte Cadet 2, with which it communicates through small dissolution pockets. It is also only one hundred meters away from grotte Blanchard (Stoetzel *et al.* 2016b) and grotte Blanchard 2 (Mallye *et al.* 2018). Abri Cadet 3 was discovered by C. Stouvenot in 2003 who conducted a test-pit excavation in its sediment in 2004 (Stouvenot *et al.* 2014). This initial excavation revealed a stratigraphy covering the Late Pleistocene and Holocene, as well as an Amerindian archaeological layer dated to the Late Ceramic period. The different layers contained a significant assemblage of small vertebrate remains. To investigate the anthropic character of some layers below the previously identified Late Ceramic layer, a detailed excavation employing a fine décapage technique was conducted by A. Lenoble in 2018 and 2019 adjacent to the first test pit (Fig. 1B). This new excavation focused on the three members of the 2004 survey's stratigraphy (Fig. 2): the lower member of silty carbonate sands deposited by runoff, the middle member of brown silt with calcareous granules and lenses of pebble, rich in crab remains and gastropod shells, and the upper member containing elusive archaeological traces from the Troumassoid period (Stouvenot *et al.* 2014).

Sedimentary and pedological signatures clarify the formation processes of the middle member, with an organic paleosol at the base covered by a poorly stratified sediment including lenses of sorted material (gravels and small pebbles) and erosional features in the upper part, indicative of debris flows and runoff deposits (Fig. 2; Table 1). The excavation also revealed that the chromatic and textural variations of

the summit part of the lower member expressed an alteration of the deposit due to the accumulation of phosphates, associated with a sedimentation gap. These findings led to the renaming of the previously identified sedimentary layers as 1 to 6 (the equivalence with the 2004 survey is shown in Table 1). Additionally, the small charcoal lenses described in the middle assemblage in 2004 were found in the paleosol (buried organo-mineral horizon) of layer 4. Examination in thin sections revealed that they correspond to *in situ* combustion structures associated with washed ashes. Finally, systematic water sieving of the entire sediment using a fine mesh resulted in the collection of small flint flakes from the middle part of Layer 4, providing evidence of human use of the shelter as early as this level. The age of the deposit's formation has been newly documented through the dating of individual charcoals contained in the pebbly lenses (layer 3) or the small charcoal lenses (layer 4). Incorporating these dates into an age-depth model, along with those obtained from the 2004 survey (Stouvenot *et al.* 2014; see Figure 2 for details and lab codes), confirms the presence of a hiatus between the formation of the lower and middle members. It also indicates that the formation of the middle member is discontinuous. The middle part of layer 4 is precisely dated by one of the samples (Lyon-15657 (GrM)). This date establishes a *terminus post-quem* for the human use of the site at 4860-5040 cal. BP, during the Archaic age, and contemporaneous with the first traces of anthropization of the island inferred from paleoenvironmental studies (Siegel *et al.* 2015).

MATERIAL AND METHODS

SUBFOSSIL BONE SAMPLE

The herpetofaunal bone sample studied is a sub-sample of the material collected during the 2018/2019 excavation. It comes from the F3c square, for which the entirety of the sediment has been sampled and water sieved with 2 mm meshes to recover most bone elements of small vertebrates. All the herpetofaunal remains collected in the F3c square during both the 2018 and 2019 excavation sessions have been studied, but only the fish, bat, and bird remains collected in the 2018 excavation

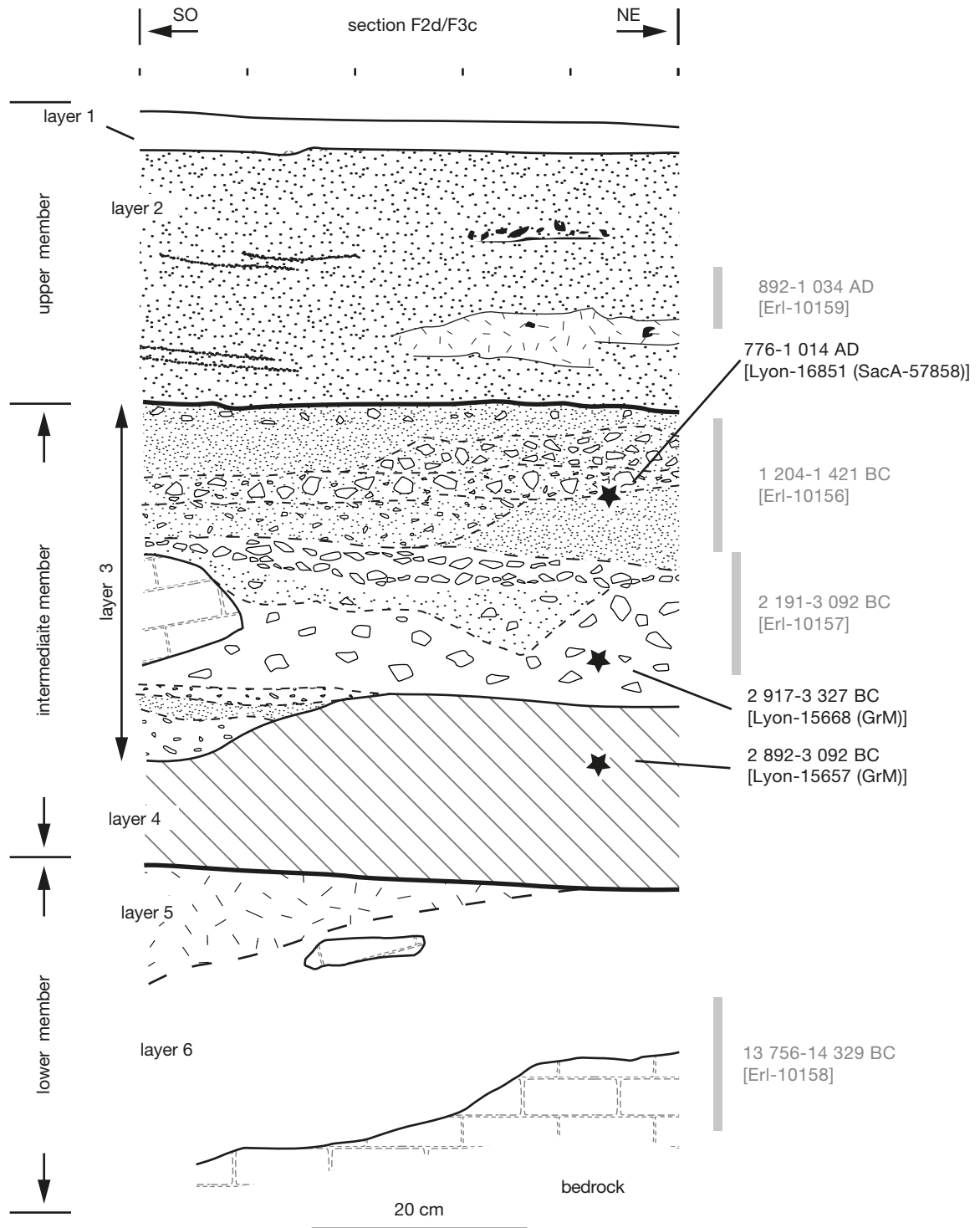


FIG. 2. — Stratigraphy of the Cadet 3 deposit following the results of the 2018/2019 excavation. **Stars** indicate the newly performed dates and grey bars the 2004 dates with the uncertainty regarding the origin of the dated material and their lab codes. The dated material is charcoal for all dates except Erl-10157 and Erl-10158 that were done on assemblages of small vertebrate bones. All the dates have been calibrated with the Intcal20 curve except the date Erl-10157 that was calibrated with the Mixed20 curve because the dated material was a mix of marine and terrestrial fauna. The correspondences between the layers indicated on the figure and the stratigraphic units identified in 2004 are indicated in Table 1.

session have been quantified so far (Table 2). Invertebrate shells have been studied from a subsample of sediment from each layer. The complete herpetofaunal assemblage consists of 10 972 squamate and amphibian bones, which are the

subject of the present taphonomic analysis. This material is currently under study at the University of Bordeaux (France) and will later be stored at the office of the Service Régional de l'Archéologie de Guadeloupe (Basse-Terre, Guadeloupe).

TABLE 2. — Number of identified individual faunal bone and shell remains in the different stratigraphic layers of the F3c square of the Cadet 3 rock shelter (in the sample collected in 2018). The counts of Mollusca are an approximation of the content of each layer based on the fractions of the complete sample studied.

Layer	1	2	3	4	5	6	Total
Pisces	5	32	3	4		3	47
Aves	6	77	163	360	443	72	1121
Chiroptera	3	30	58	216	167	233	707
Amphibia	3	12	16	48	57	38	174
Squamata	31	528	1179	1810	2755	4495	10798
Unidentified Vertebrata	17	261	545	459	1131	497	2910
Mollusca	212	2872	2540	1124	22	46	6816
Total	277	3812	4504	4021	4575	5384	22573

TAXONOMIC IDENTIFICATION

The herpetofaunal species of the Guadeloupe islands were identified following published anatomical criteria for frogs (Bochaton *et al.* 2015), lizards (Bochaton *et al.* 2017, 2018, 2019a, 2021a), and snakes (Bochaton & Bailon 2018; Bochaton *et al.* 2019b). When no criteria were available, fossil specimens were compared to the following osteological modern specimens stored at the University of Bordeaux (<https://pacea-collections.inist.fr>): *Anolis roquet* (Bonnaterre, 1789) (PACEA-H-0008 and PACEA-H-0009), *Ameiva plei* Duméril & Bibron, 1839 (PACEA-H-0038), *Hemidactylus mabouia* (Moreau De Jonnès, 1818) (PACEA-H-0039), and *Iguana iguana* (Linnaeus, 1758) (PACEA-H-0018).

The number of identified skeletal parts (NISP) for each taxon has been considered, and a minimal number of individuals (MNI) has been estimated following Poplin (1976). The size of *Anolis* lizards has been estimated based on the following measurements taken on the fossil bones by a single user (M.S.): length of the dentary and maxillary dental rows, ilium greater height and humerus proximal width. Equations used are those of Bochaton & Kemp (2017) and the general protocol is that of Bochaton *et al.* (2017). The size estimation of the individuals present in the assemblage will allow for the description of the subfossil population present in the cave (e.g. only large adult specimens, natural population with many juveniles, juveniles only). This will help investigate the accumulation processes of the bone assemblage and describe the selective practices of the putative accumulator agent(s).

TAPHONOMIC ANALYSIS

The anatomical distribution of the remains was studied using the Percentage of Representation (PR) of Dodson & Wexlar (1979). Fragmentation of each individual bone was recorded using a percentage of completeness (0-5%, 5-25%, 25-50%, 50-75%, 75-90%, 90-99%, and 100%). Sub-complete bones correspond to fragments between 75% and 100% of completeness. In the case of long bones, the part of the bone corresponding to the fragment was also recorded (complete bone, proximal part, distal part, diaphysis, proximal epiphysis, distal epiphysis), as well as its maturity stage (epiphyses unfused, fused proximally, fused distally, fully fused). For all investigated bones, the occurrence and intensity of digestion traces were recorded according to the protocol of Stoetzel *et al.* (2021). The same criteria as those described by Stoetzel *et al.*

(2021) were followed to describe the digestion intensity of the dentaries and long bones (absent, low, moderate, high intensity). Additionally, observations were made on other elements such as: vertebrae and all cranial bones. On vertebrae, the same traces as those described by Lev *et al.* (2020) were observed. The digestion stages recorded on vertebrae correspond to the occurrence of digestion traces, and the intensity of alteration of the global shape of the vertebrae. In low intensity digestion, only the articular parts are slightly digested, while in moderate intensity, the other areas of the vertebrae show clear marks of dissolution. In high intensity digestion, the general shape of the bone is altered, and some areas are completely destroyed. The same stages apply to cranial elements, with the only difference being that the low intensity stage is more difficult to record on bones lacking large articular surfaces, whose cortical bone is very thin and often altered in low intensity digestion. The occurrences of other taphonomic surface alterations, including possible anthropic origins such as cut marks and fire traces were also noted. All surface observations were performed using a binocular microscope (Nikon SMZ1000).

STATISTICAL ANALYSIS

Statistical analyses were conducted using the software R (www.r-project.org) and R studio (version 4.0.3) (RStudio 2015), mostly using the base package “stats”. Pairwise Chi² or Fisher test analyses with Bonferroni corrections were used to detect differences in bone counts between layers regarding vertebrate taxonomic composition, anole bone anatomical distribution, and fragmentation. Kruskal-Wallis tests were used to detect anole’s size variations between layers, and the Gaussian Mixture Models used to analyze anole size data were performed using the package Mixtool (Young *et al.* 2016). P-values below 0.05 were considered significant.

ABBREVIATIONS

- MNI minimal number of individual;
- NISP number of identified skeletal parts.

RESULTS

TAXONOMIC COMPOSITION OF THE FULL FAUNAL SAMPLE

The full sample collected in 2018 in the F3c square consists of 11 982 vertebrate remains, of which 9 075 have been taxo-

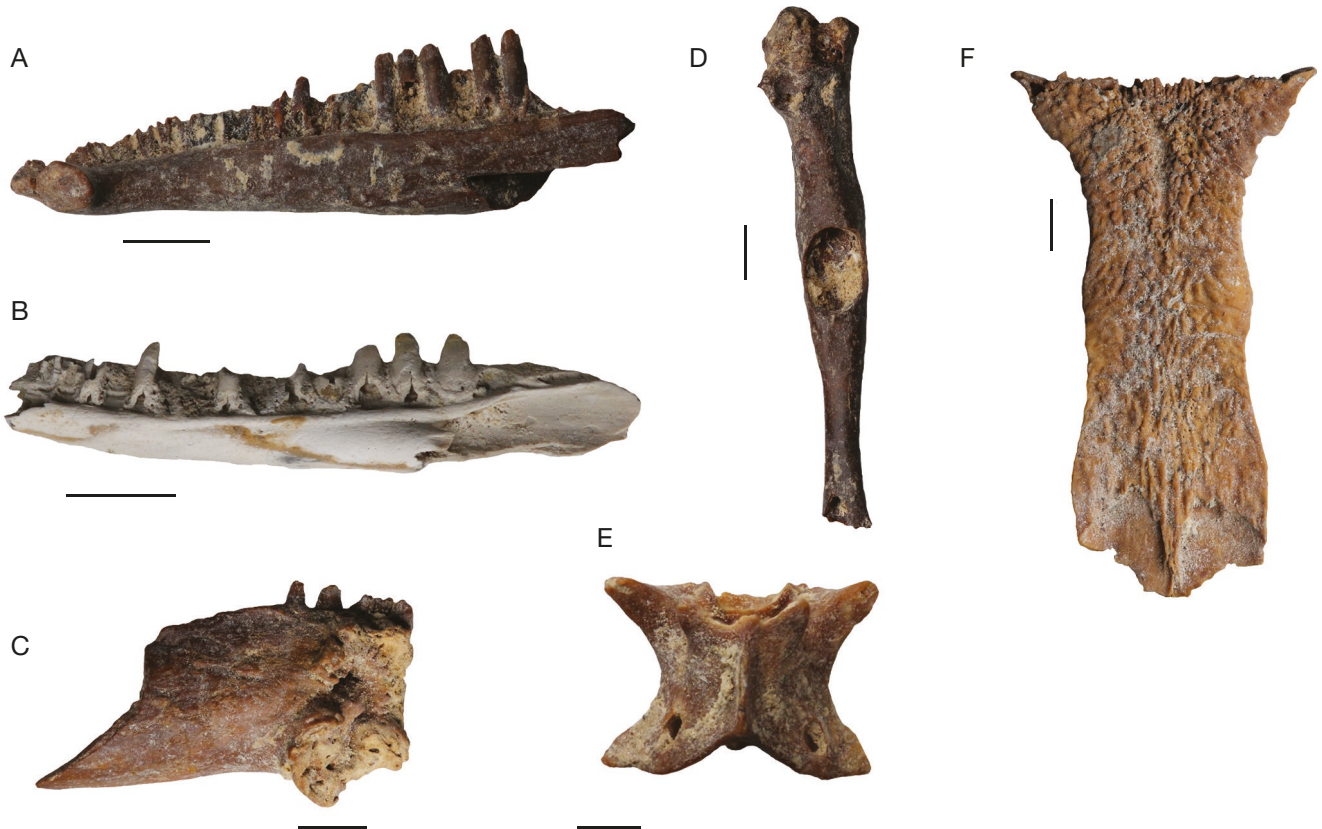


FIG. 3. — Pictures of the herpetofaunal subfossil bones studied from the Cadet 3 rock-shelter: **A**, right dentary of *Anolis* Daudin, 1802 presenting digestion traces of moderate intensity; **B**, right dentary of *Anolis* presenting burning traces; **C**, right dentary of *Anolis* presenting traces of a healed fracture located near the posterior end of the dental row; **D**, femur of *Anolis* presenting a geographic osteolysis (possibly a bone tumor); **E**, trunk vertebra of *Alsophis* sp. presenting digesting traces of strong intensity; **F**, frontal bone of *Pholidoscelus turukaeraensis* Bochaton, Boistel, Grouard, Ineich, Tresset & Bailon, 2017. Scale bars: 2 mm.

nomically identified, and 6816 invertebrate shell remains (Table 2). Among the identified vertebrate bones, 7111 (78% of the NISP) were attributed to squamates, 1121 (12.3%) to birds, 707 (7.8%) to bats, 83 (0.9%) to amphibians, and 47 (0.3%) to fishes (Table 2). Squamate bones represent at least 60–70% of the NISP in nearly every layer, bird remains around 12–20%, but reach over 39% in layer 4 and drop to 1.6% in layer 6. Fish remains are more numerous in layers 1 and 2 (10% and 5% of the vertebrate NISP, respectively) and are nearly absent from the oldest layers. Bat remains represent around 5% of the bone counts except in layer 4 where they reach 20%. The distribution of the vertebrate taxa appears to be statistically different between the layers, as indicated by the results of pairwise Chi² tests ($p_{\text{val}} < 0.05$).

Among the 10974 herpetofaunal remains recovered in 2018 and 2019 and analyzed here, ten taxa were identified. *Anolis* cf. *ferreus* (Cope, 1864) represents the majority of the herpetofaunal assemblage (89.3% of the number of remains) (Fig. 3A–D) and is present in every layer similarly to a small frog *Eleutherodactylus* sp., and *Pholidoscelus turukaeraensis* (Bochaton, Boistel, Grouard, Ineich, Tresset & Bailon, 2017) (Fig. 3F). *Capitellum* cf. *mariagalantae* (Hedges & Conn, 2012), *Antilotyphlops* sp., and *Alsophis antillensis* (Schlegel, 1837) were present in all layers except layer 1. *Alsophis* sp. 2 described by Bochaton *et al.* (2019b), was only observed in layer 6. *Thecadactylus rapicauda* (Houttuyn, 1782) was found

only in layers 2, while *Leiocephalus* sp. remains were only found in layers 2 and 3, and *Boa blanchardensis* (Bochaton & Bailon, 2018) was recovered from layers 5 to 6 (Table 3). Variations in proportions are apparent, such as the higher proportion of *Pholidoscelus turukaeraensis* in layer 4. However, the distribution of the bones of the different taxa across the layers did not enable us to draw statistically significant differences between the layers, following the results of pairwise Fisher tests with Bonferroni corrections ($p_{\text{val}} > 0.05$).

BODY SIZE OF SUBFOSSIL INDIVIDUALS OF *ANOLIS* CF. *FERREUS*
The measurements collected on the different anatomical parts considered allowed for 320 body size reconstructions, representing at least 73 individuals. No size difference has been observed between the different layers (Kruskal-Wallis test; $p_{\text{val}} > 0.05$).

The distribution of the estimated size was unimodal (Fig. 4), with a minimal estimated SVL of 48.3 mm and a maximal of 148.9 mm. The mean size of the anoles from the assemblage is 98.4 mm. Using the estimations from the humerus with fused proximal epiphysis ($N = 18$), it was estimated that the size of mature individuals ranges from 62.8 mm to 141 mm, with a mean of 106.1 mm. The distribution of the 18 mature estimated SVL presents a clear bimodality probably related to sexual dimorphism previously recorded in similar assemblages (Bochaton *et al.* 2017).

TABLE 3. — Number of identified skeletal parts (NISP) and minimal number of individual (MNI) of the squamate and amphibian taxa identified in the different stratigraphic layers of the Cadet 3 rock shelter.

Layer Taxa	1		2		3		4		5		6		Total	
	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI
<i>Eleutherodactylus</i> sp.	3	1	12	2	16	2	48	3	57	9	38	4	174	21
<i>Thecadactylus rapicauda</i> (Houttuyn, 1782)	–	–	2	1	–	–	–	–	–	–	–	–	2	1
<i>Anolis</i> cf. <i>ferreus</i>	27	2	457	10	1024	33	1664	43	2525	38	4102	49	9799	175
<i>Leiocephalus</i> sp.	–	–	3	1	1	1	–	–	–	–	–	–	4	2
<i>Pholidoscelis turukaeraensis</i> Bochaton, Boistel, Grouard, Ineich, Tresset & Bailon, 2017	3	1	18	2	59	7	45	4	19	1	73	4	217	19
<i>Capitellum</i> cf. <i>marialagante</i>	–	–	9	1	22	1	5	1	4	1	18	1	58	5
Unidentified Lacertilia	1	–	3	–	2	–	6	–	1	–	1	–	14	–
<i>Alsophis</i> sp. 2	–	–	–	–	–	–	–	–	–	–	1	1	1	1
<i>Alsophis antillensis</i> (Schlegel, 1837)	–	–	9	1	17	1	8	1	13	1	24	1	71	5
<i>Boa blanchardensis</i> Bochaton & Bailon, 2018	–	–	–	–	–	–	–	–	4	1	12	1	16	2
<i>Antilotyphlops</i> sp.	–	–	2	1	4	1	3	1	–	–	1	1	10	4
Unidentified Squamata	–	–	25	–	50	–	79	–	189	–	263	–	606	–
Unidentified Vertebrata	–	–	–	–	1	–	–	–	–	–	1	–	2	–
Total	34	4	540	19	1196	46	1858	53	2812	51	4534	62	10974	235

TABLE 4. — Bone counts (in NISP) and their percentages of bone completeness for the different anole anatomical parts in the subfossil assemblage of Cadet 3.

Bone completeness %	Mandible	Skull	Dorsal vertebrae	Caudal vertebrae	Anterior limbs	Posterior limbs	Girdles and extremities	Total
0-5	1	8	–	–	1	–	–	10
5-25	261	622	13	15	117	202	182	1412
25-50	212	484	509	43	70	78	138	1534
50-75	175	682	262	121	59	60	194	1553
75-90	253	1145	826	856	70	75	241	3466
90-99	127	293	884	367	39	37	18	1765
100	1	7	7	1	–	2	1	19
Mean	44,53	50,07	67,21	74,50	39,46	33,29	43,74	55,72

TABLE 5. — Taphonomic alterations observed on the full herpetofaunal assemblage of Cadet 3.

Layer	1	2	3	4	5	6	Total
Absence of trace	32	386	940	1317	2969	4592	10236
Digestion (low)	2	50	105	103	244	176	680
Digestion (moderate)	–	–	8	3	11	10	32
Digestion (strong)	–	2	6	1	13	4	26
Total	34	438	1059	1424	3237	4782	10974
Burning traces	–	10	16	19	7	–	52

TAPHONOMIC ANALYSIS OF THE HERPETOFAUNAL REMAINS
 As *Anolis* remains account for 90% of the bone assemblage, and the bone counts of the other taxa are mostly below 100 it was not possible to consider all the species in a taphonomic quantitative approach, as no significant results could be drawn from such low counts. Herpetofaunal taxa present very diverse morphological characteristics, and it is thus not possible to mix several species from different families in a single analysis. As such, the quantitative aspects of the taphonomic analysis will focus on *Anolis* remains.

Regarding the anatomical distribution of the anole bone remains, all anatomical parts were represented. The assemblage had a high relative PR of maxillary and dentary bones in relation to other skull and post-cranial elements (Fig. 5). Among post-cranial elements, the largest bones (femur and humerus: PR = 52.5% and 43.8%, respectively) are the best represented, followed by vertebrae (PR = 31.7%), tibiae (PR = 19%), and girdles (PR = 10% to 18%). Radius elements were very scarce in the assemblage, probably because the identification of their diaphysis fragments is very challenging. Ulna remains

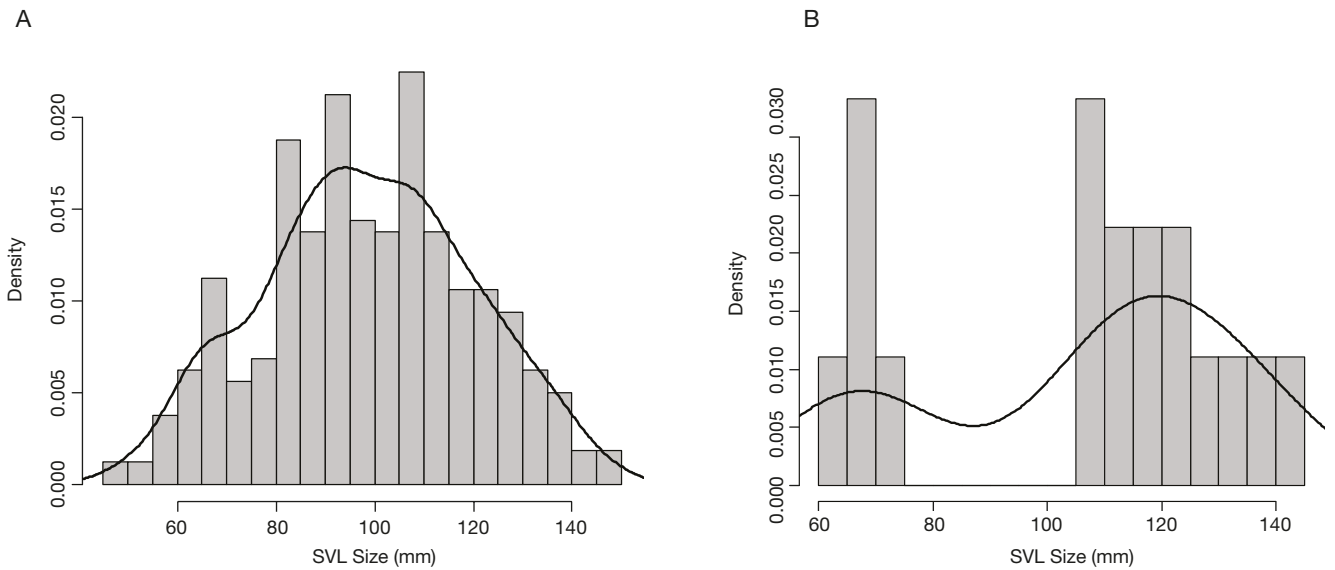


FIG. 4. — **A**, Snout-Vent Length estimations obtained on all measured *Anolis cf. ferreus* bone remains in the Cadet 3 assemblage (N = 320; MNI = 73); **B**, *A. ferreus* adult individual SVL size estimations provided by the measured fully fused humerus bone from the Cadet 3 subfossil assemblage (N = 18; MNI = 9).

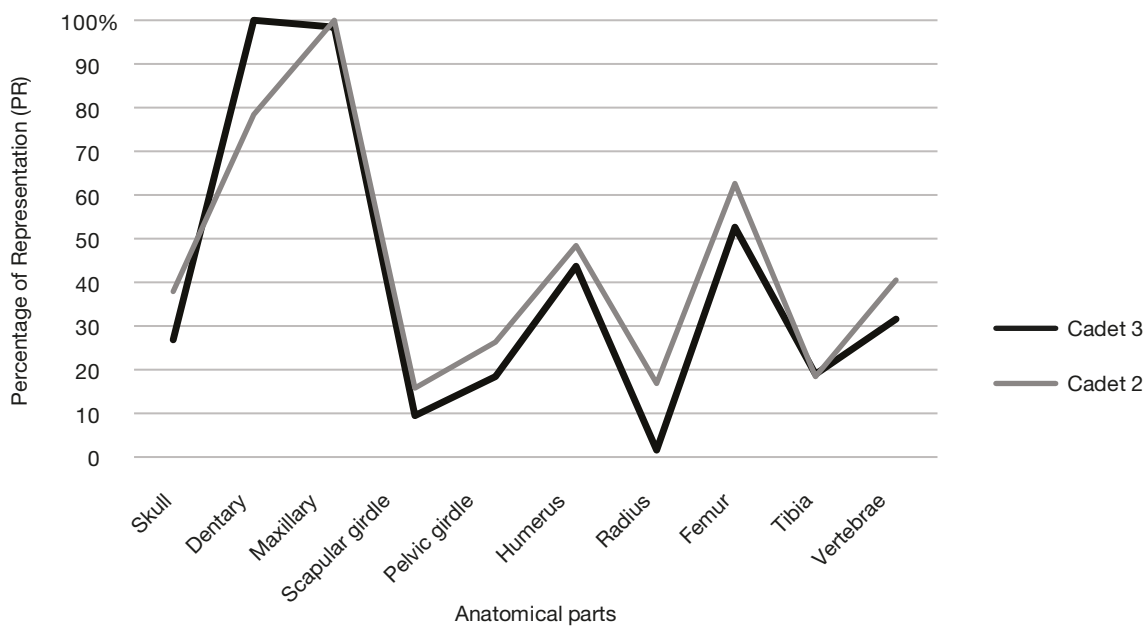


FIG. 5. — Comparison of the percentages of representation (PR) of the different *Anolis cf. ferreus* anatomical parts collected in the studied herpetofaunal assemblage of the Cadet 3 and the Cadet 2 sites.

were too scarce in the assemblage to be worth considering. A pairwise χ^2 test (p -val > 0.05) showed no significant difference between the layers. Regarding fragmentation, thoracic vertebrae, and caudal vertebrae had the highest completeness mean (67.2% to 74.5%), with 68.6% and 87.2% of them being sub-complete to complete. Conversely, long bones are the most fragmented elements, with a completeness mean of 39.4% to 33.2% with 30.6% to 25.1% of the bone being at least sub-complete (Table 4). χ^2 pairwise tests showed no significant differences between layers regarding bone fragmentation (p -val > 0.05). The overall bone completeness mean is 55.7%.

The results remain the same when unidentified lizard bones are added to the analysis, showing that putative identification bias (i.e., tibiae and radius) does not impact these observations.

Most herpetofaunal remains (93%) presented no trace of any taphonomic alterations on their surface (Table 5). Most of the taphonomic alterations observed were digestion traces which were present on 2.2% to 13.1% of the remains in most layers. However, layers 4-5 had more digested remains (23.5% of anole bones presented such alteration). Most of the digestion traces observed (93.5%) matched a low intensity, and only a few remains were attributed to moderate (3.8%) (Fig. 3A)

or high (2.6%) (Fig. 3E) digestion intensity. Digestion was most frequently observed on trunk vertebrae (48.2% of the observations) or caudal vertebrae (29.6% of the observations), whereas other anatomical parts accounted for 1.8% to 8.5% of digested remains. No Chi² test could be carried out because of the limited occurrence of bone remains presenting taphonomic alterations in the different layers. Regarding traces of possible anthropic origin, between 1.4% and 0.1% of the bone remains presented putative burning traces in most stratigraphic layers (Fig. 3B), however, layer 2 presented a higher proportion of such alteration with 3% of its bone remains being burned. There is, however, no indication that these traces correspond to intentional burning of the bones. No other possible anthropic alterations were observed in the assemblage. Some observations could also be made regarding the pathologies of *Anolis* specimens such as a fractured dentary probably broken during a male fight (Fig. 3C) or a femur presenting a thickening of its cortical bone and a geographic osteolysis, possibly a bone tumor (Fig. 3D).

DISCUSSION

GENERAL REMARKS ON THE ASSEMBLAGE

From a qualitative standpoint, the herpetofaunal taxonomic composition of the assemblage does not exhibit any unique characteristics compared to previously published nearby assemblages (Stouvenot *et al.* 2014; Bailon *et al.* 2015; Bochaton *et al.* 2015) and aligns with the existing understanding of the temporal evolution of the Marie Galante herpetofaunal assemblage (Bochaton *et al.* 2021b). The primary significance of the new material from Cadet 3 lies in the taphonomic approach undertaken and its relevance in identifying the accumulator agents responsible for the formation of the assemblage. The composition of the assemblage remains stable in terms of the consistent over-representation of *Anolis* remains throughout the sequence. However, the distribution of other taxa exhibits notable variations, likely indicating changes in the site's environment and/or accumulation processes. A comprehensive taxonomic and taphonomic analysis of the entire bone assemblage would be necessary to address this question.

IDENTIFICATION OF THE ACCUMULATION AGENT

The possibility that the accumulation of herpetofaunal taxa, especially anoles, reflects natural mortality inside the cave can be ruled-out based on the following reason: 1) the presence of digestion traces in the material; 2) *Anolis ferreus* being primarily an arboreal species, unlikely to be found in high numbers in a rock shelter (Breuil 2002; Henderson & Powell 2009); and 3) the predominance of large individuals above 80 mm SVL in the assemblage, which does not align with a natural mortality profile. These factors indicate the involvement of an accumulator agent in the creation of the herpetofaunal assemblage. The contribution of human groups can also be disregarded, as indigenous groups have been documented on Marie Galante since approximately 5 000 BP (Siegel *et al.* 2015; this study), but there is no evidence of human consumption

the studied squamate and amphibian specimens. The absence of variation in accumulation processes time suggests that the accumulator agent was already present in the cave since the Late Pleistocene, preceding the arrival of humans set foot on Marie Galante. Additionally, no tool traces were found on the bone remains, and the limited occurrence of burnt remains (0.5% of the herpetofauna NISP) may have accidental origins, commonly observed in cave contexts (Stoetzel *et al.* 2011). Therefore, the most plausible explanation for the accumulation and the presence of digestion traces is the involvement of a non-human accumulator agent. The scarcity of digestion traces, their low intensity, the absence of gnawing marks, and as relatively low degree of fragmentation in the assemblage argue against the role of a mammalian predator (Andrews 1990) which were likely absent from the island prior to human arrival, as it is supported by biogeographic and paleontological evidence (Lorvelec *et al.* 2007; Stouvenot *et al.* 2014; Stoetzel *et al.* 2016b). Given that snakes digest bones (Stahl 1996) and carnivorous bats are not present in the area, the remaining possible predators are raptors, specifically nocturnal raptors, as diurnal raptors tend to cause more extensive bone breakage and digestion in their accumulations (Errington 1930; Kusmer 1990).

Regarding taphonomic evidence, the anatomical distribution of the remains exhibits a “typical owl pattern,” characterized by the prevalence of cranial, mandibular, postcranial axial bones, and long bones (femur, tibia, and humerus), which is also observed in small mammals preys assemblages (Stoetzel *et al.* 2011). The presence of all anole skeletal parts, along with as the over-representation of teeth bearing elements, aligns with the hypothesis of an owl bringing complete prey items into the rock shelter (Dodson & Wexlar 1979; Stoetzel *et al.* 2021). The low fragmentation of the anole assemblage, with a mean bone completeness of 55.72% and up to 30% being complete depending on the layer, correspond to the behavior of an owl swallowing its prey whole, especially considering the high potential for post-depositional bone fragmentation in fragile herpetofauna bone elements (Llona & Andrews 1999; Stoetzel *et al.* 2012). The overall level of overall digestion in the material is also consistent with that of a category one predator, specifically an owl, as defined by Andrews (1990).

In addition to the taphonomic observations other characteristics of the accumulation support the hypothesis of an owl as the accumulator agent.

The significant representation of *Anolis ferreus* in the assemblage suggests that hunting occurred mainly on tree branches but also occasionally on the ground, as indicated by the presence of strictly terrestrial taxa such as *Pholidoscelis turukaerensis* and *Capitellum cf. mariagalantae* (Henderson & Powell 2009). This pattern aligns with a flying predator hunting in dense forest areas with limited opportunities to capture prey on the ground. The presence of diurnal taxa in the assemblage is not surprising since Caribbean owls can hunt during the day and at dusk, coinciding with the period when anoles are less active. Anoles, for example, sleep on branches and remain still, making them an easy prey (Buden 1974; Stoetzel *et al.* 2016a). The concentration of anole remains in the Cadet 3

assemblage further indicates a highly specialized hunting behavior, which is consistent with the range of behaviours observed in Caribbean owls (Stoetzel *et al.* 2016a, 2021).

Currently, no owl species inhabits the Guadeloupe Islands. The Lesser Antillean barn owl *Tyto insularis* (Pelzeln, 1872), a medium-sized barn owl, has been proposed as a potential accumulator agent in grotte Blanchard (Gala & Lenoble 2015; Stoetzel *et al.* 2016b). Another owl, *Tyto cf. noeli*, has been identified in Guadeloupe (Gala *et al.* 2022). Fossil evidence from Cuba suggests that this giant owl may have consumed small squamates (Suárez & Diaz-Franco 2003; Syromyatnikova *et al.* 2021), but it appears to have primarily hunted larger endemic rodents of the Oryzomini tribe (Steadman & Hilgartner 1999; Suárez & Olson 2015; Gala *et al.* 2022). Furthermore, the historical occurrence of this owl on Marie Galante is uncertain. This extinct owl is believed to have preyed on native mammals of the Oryzomini tribe, which are absent from the fossil record of Marie Galante prior to human occupation of the island. However, in the fossil assemblages of Cadet 3 and nearby deposits, several bones of a smaller owl, *Athene cunicularia guadeloupensis* (Ridgway, 1874), have been identified (Gala *et al.* 2021). In Cadet 3, bones of this raptor are present throughout the stratigraphy, including juvenile specimens, indicating that these owls used the cave as a nesting site. *Tyto insularis* and *A. cunicularia guadeloupensis* could potentially be accumulator agents for the Cadet 3 assemblage. The taphonomic signature of these two taxa is somewhat similar and varies depending on the site, taxa, and anatomical part considered (Montalvo *et al.* 2020; Stoetzel *et al.* 2021). In general, both owls produce minimal bone fragmentation, with 50% to 97% of the bones being complete in their respective assemblages. Digestion traces are well represented, present in 50% to 90% of the material, but are mostly of light intensity (approximately 75% for *A. cunicularia* and 90% for *T. insularis*). The level of digestion intensity in the Cadet 3 fossil material is similar, but such traces are only present on 7% of the fossil assemblage. Notably, the fossil assemblage exhibits stronger fragmentation, with only 30% of the bones being complete. These differences could be attributed to post-depositional processes affecting fragmentation and intra-specific variability in digestion. Nevertheless, based solely on taphonomic information, it is not possible to definitively attribute the constitution of the assemblage to either of these two owls. The sizes of the subfossil anoles from Cadet 3 enable rough estimations of their weight, which fall below 30–40 g according to Schoener (1969) work. This makes even the largest specimens potential prey for *A. cunicularia*, whose maximum prey weight is estimated to be around 115 g (Schlatter *et al.* 1980; Montalvo *et al.* 2020), as well as for *T. insularis*, which is a larger owl. *Athene cunicularia* is known to hunt throughout a 24 hour period, which would allow encounters with anoles (Montalvo *et al.* 2020; Poulin *et al.* 2020), and *T. insularis* has already been observed hunting anoles (Stoetzel *et al.* 2016a). Both of these owls are opportunistic and generalist predators that can feed on herpetofaunal prey, and in some cases, even exhibit a dependency on a single taxon (Bellocq 1987). Considering their past

occurrences and biological characteristics, they could serve as suitable accumulator agents for the herpetofaunal accumulation in Cadet 3. However, it should be noted that our approach does not rule out the possibility that some of the large specimens from the anthropic layers of Cadet 3, which apparently lack digestion traces, may have been collected by humans for consumption (e.g. *Pholidoscelis* lizards). Nonetheless, no taphonomic evidence supports this hypothesis. In any case, the very limited occurrence of taphonomic evidence potentially associated with human activities indicates that this phenomenon would be minor in terms of its contribution to the overall herpetofaunal assemblage.

THE OTHER HERPETOFAUNAL BONE ASSEMBLAGES OF MARIE GALANTE

Regarding the two nearby similar subfossil deposits: Cadet 2 (Bochaton *et al.* 2015) and Blanchard (Bailon *et al.* 2015), if *Athene cunicularia* is responsible for the herpetofaunal bone accumulation in Cadet 3, what can be said about these sites? The taxonomic composition of Cadet 2 and Blanchard is similar to the Cadet 3 assemblage, but there are notable variations. In grotte Cadet 2, ten herpetofaunal taxa were found and eleven in grotte Blanchard, with a different repartition from the one observed in Cadet 3. Indeed, *Eleutherodactylus* Duméril & Bibron, 1841 represents 84.1% of the studied herpetofaunal assemblage of Cadet 2, and *Anolis ferreus* only 15% (Bochaton *et al.* 2015). However, in grotte Blanchard, *Anolis ferreus* is the most common taxon (42.1%), along with *Eleutherodactylus* sp. (31.1%) (Bailon *et al.* 2015).

In grotte Blanchard, half of the anole remains were found in a single layer (C5), where they represent 78% of the herpetofaunal remains. Additionally, frog remains are more numerous in layers C12 and C8, where 54% of the 1177 remains belonged to *Eleutherodactylus* (accounting for 58% of the frog remains from the site). Digestion traces were reported on amphibians and significant portion of anole, ameiva, and small snake remains. The frequency and intensity of these traces are consistent with predation by an owl (Bailon *et al.* 2015). *Athene cunicularia* could have preyed upon these taxa, but it is possible that multiple accumulation processes overlapped as some taxa would be too large to be preyed upon by this small owl, suggesting the involvement of a larger predator (e.g. *Tyto insularis*) (Stoetzel *et al.* 2016a) or other phenomena such as the cave being occupied by boid snakes hunting bats (Arendt & Anthony 1986; Rodriguez-Duran 1996; Angin 2014). A detailed taphonomic analysis is still lacking to further explore these questions. In grotte Cadet 2, anoles and frogs were abundant in all layers, with most anatomical parts recovered (Bochaton *et al.* 2015). A taphonomic study of this assemblage was conducted as part of a Master's dissertation (Bochaton 2013) but remained unpublished. This study provided anatomical distribution data for anole bones (Fig. 5) and frog remains. The anatomical distribution of anole bones is similar to that observed in Cadet 3. A high percentage of digestion traces was observed on anoles, with 50% of the vertebrae bearing digestion marks and 30% of the frog humeri. Frog bones exhibited strong

fragmentation, but the variability across anatomical parts (ranging from 21% to 64% of complete humer and almost no complete ilia) suggests post-depositional fragmentation rather than the involvement of an accumulator agent. Anole dentaries exhibited variable fragmentation depending on the layer, with complete bones ranging from 41% and 7%, which is similar to Cadet 3 (ranging from 8% to 35%).

The limited taphonomic evidence available from grottes Cadet 2 and Blanchard suggests several different accumulation modes. An owl (possibly *A. cucularia*) might be responsible for the accumulation of frog bones, considering the low fragmentation and moderate intensity of digestion traces observed. However, the lack of a modern comparative sample hinders further investigation of this question. For anoles, as carnivores were absent from the island during that time, a diurnal raptor such as a falcon or hawk (Powell & Henderson 2008) may have contributed to the accumulation in Cadet 2, with a higher proportion of digestion traces compared to Cadet 3. Other phenomena, such as boid snakes visiting the cavities to feed on bats, might explain the accumulation of larger herpetofaunal species (Bailon *et al.* 2015; Bochaton & Bailon 2018).

CONCLUSION

Our detailed taphonomic study provides evidence supporting the role of *A. cucularia* in the formation of the herpetofaunal assemblage in Cadet 3, while excluding the possibility of a significant human involvement. This finding is significant as it contributes to a better understanding of the prey sampling range and prey selection of the predator, thus enhancing our understanding of the faunal assemblage in term of paleobiodiversity. The site of Cadet 3 is notable for the consistent accumulation processes observed in its herpetofaunal assemblage, which appear to have remained stable from the Late Pleistocene to the Amerindian period. However, comparisons with other faunal assemblages on Marie Galante reveal more complex scenarios with the involvement of different accumulator agents, and possibly multiple agents within the same sites. It is essential to replicate the type of taphonomic study conducted in Cadet 3 should now be replicated on other assemblages in Marie Galante and throughout the Caribbean to improve our overall understanding of the paleobiodiversity in this region. Additionally, neotaphonomic investigations are urgently needed to facilitate more accurate interpretations of accumulation modes in archaeological and palaeontological sites.

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