



**From a thriving past to an uncertain future:
Zooarchaeological evidence of two millennia of human
impact on a large emblematic lizard (*Iguana
delicatissima*) on the Guadeloupe Islands (French West
Indies)**

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Title: From a thriving past to an uncertain future: zooarchaeological evidence of two millennia of human impact on a large emblematic lizard (*Iguana delicatissima*) on the Guadeloupe Islands (French West Indies)

Running title: Past *Iguana* from the Guadeloupe Islands

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Abstract

Among the lizards in the Lesser Antillean Islands, iguanas are undoubtedly the most emblematic, especially the endemic species, *Iguana delicatissima*. However, although much effort is currently made for the conservation of this species as a result of the present biodiversity crisis, nearly

nothing is known of the history of this animal on these islands during the last millennia. Here we present the first data relating to the distribution, morphology, and interaction of past iguanas with human populations in the Lesser Antilles. To do so, we review the archaeological *Iguana* remains collected over the past 15 years on the Guadeloupe Islands. Our results show that the only *Iguana* species occurring in pre-Columbian archaeological deposits is *Iguana delicatissima*. Moreover, we demonstrate that this species occurred on all the islands of Guadeloupe during pre-Columbian times and then suddenly became extinct between 1960 and 1990 on most of these islands. We also confirm the modern introduction of *I. iguana* to the Guadeloupe Islands. In addition, zooarchaeological research demonstrates that pre-Columbian human populations occasionally used iguanas as a source of food, but with no apparent impact on the native population. However, the first data relating to past size variations of *I. delicatissima* on the Guadeloupe Islands indicate that archaeological iguanas were much larger than the largest remnant modern specimens and that a marked decrease in body length (more than 20%) occurred in these lizards after contact with European populations. This evidence of widespread extinction and morphological change during modern times is another demonstration of the extensive effects of disturbance and selection induced by modern human societies on endemic insular faunas.

1. Introduction

The fauna of the Lesser Antilles Islands is rich in lizards and snakes with a high degree of endemism (Henderson and Powell, 2009; Henderson and Breuil, 2012). However, due to the small size and ecological sensitivity of these islands, squamates are, like many other vertebrate taxa, strongly impacted by the current worldwide biodiversity crisis (Barnosky et al., 2011). The islands of Guadeloupe are no exception to this, and both historical (Breuil, 2002; Breuil et al., 2011, 2010) and fossil data (Bailon et al., 2015; Bochaton et al., 2016a, 2015; Boudadi-Maligne

et al., 2016; Grouard, 2001; Stouvenot et al., 2014) show that most of the past endemic squamates of these islands have become extinct, mainly during the recent past.

The most emblematic of the surviving reptiles is probably the genus *Iguana* Laurenti, 1768, represented by the green iguana (*Iguana iguana* [Linnaeus, 1758]), and the Lesser Antillean iguana (*Iguana delicatissima* Laurenti, 1768) (Breuil, 2002; Henderson and Breuil, 2012). These two species diverged around 22.8 Mya ago (Hedges et al., 2015) and are both present in the Lesser Antilles. However, they seem to have undergone different local evolutionary histories, although they can still breed together and produce fertile offspring (Vuillaume et al., 2015). *I. iguana* has a very broad natural distribution area in continental Central and South America (Stephen et al., 2013) and was recently (accidentally or deliberately) introduced far from its natural distribution area to many places in the world, such as Israel, Hawaii, Florida, the Greater Antilles, and the Lesser Antilles, probably including Guadeloupe (Breuil, 2013; Falcón et al., 2013; Henderson and Breuil, 2012; Krauss et al., 2014; Pasachnick et al., 2012). Endemic populations also seem to occur on some of the Lesser Antillean islands, such as Saba, Montserrat, and Saint Lucia (Breuil, 2013; Malone and Davis, 2004; Morton, 2009; Stephen et al., 2013). Conversely, *I. delicatissima* is endemic to the Lesser Antilles. It is now considered to be an endangered species on the most recent IUCN red list (Breuil et al., 2010), as it is now extinct on most of the islands in Guadeloupe (Breuil, 2002; Henderson and Breuil, 2012), and is currently the focus of an international plan of action (Knapp et al., 2014). Recent genetic data show little divergence between the different Lesser Antillean populations and suggest that this animal may have spread to the islands recently, possibly as a result of human activity (Martin et al., 2015; Vuillaume et al., 2015). This hypothesis is congruent with the paleontological results obtained from Pleistocene and Holocene fossil data from the island of Marie-Galante, which show that no

67 *Iguana* osteological remains occur in layers preceding the arrival of human populations
68 (Bochaton et al., 2015).

69 Both of these *Iguana* species can hybridize when syntopic, which probably played a major role in
70 the extinction of *I. delicatissima* in Guadeloupe, except for the islands of La Désirade and Îlets de
71 Petite Terre, where there are no *I. iguana* (Breuil, 2002). However, although this genus is absent
72 from the very sparse Pleistocene and early Holocene fossil record in Guadeloupe, historical
73 (Breuil, 2002; Du Tertre, 1667) and especially archaeological (Grouard, 2010, 2007, 2001)
74 sources provide evidence of the past occurrence of the genus *Iguana* on these islands. The latter
75 sources show that the genus *Iguana* sp. has been present on all the islands of Guadeloupe since at
76 least 1500 BC and was hunted by pre-Columbian human populations more than 2,000 years
77 before the arrival of Europeans. On account of a combination of extensive data concerning the
78 modern representative of this genus and archaeological data, the iguana is an excellent model for
79 studying the temporal evolution of human impact on insular large lizard populations.

80 Up until recently, few data concerning archaeological iguanas from the Guadeloupe Islands had
81 been recorded. Zooarchaeological studies have, in the Guadeloupe Islands and in other Caribbean
82 islands, mainly focused on the extensive biodiversity of other taxa, especially aquatic animals,
83 which largely compose the meat diet of most of past human populations rather than taxa, like
84 iguanas, that remain scarce in zooarchaeological assemblages (Giovas, 2016; Grouard, 2010;
85 Keegan et al., 2008; Wing, 2001). In addition, the paucity of research on iguanas, and more
86 generally archaeological lizard remains, has further complicated these studies. As a consequence,
87 the few studies to date of iguanas from archaeological contexts focused on the taxonomic
88 identification of osteological remains (Martin, 2009; Martin et al., 2010). These studies showed
89 that two iguana species (*I. iguana* and *I. delicatissima*) occurred on the Guadeloupe Islands

prehistorically (Martin, 2009; Martin et al., 2010); a finding that contradicts the notion that *I. iguana* would be a recently introduced species. An early occurrence of *I. iguana* was also advanced by Lazell (1973), who stated that “no human introduction is responsible for the presence of *Iguana iguana* anywhere in the Lesser Antilles”. However, the conclusions proposed by Martin (2009) and Martin et al. (2010) based on archaeological specimens are questionable, since a recent study conducted by Bochaton et al. (2016b), focusing on the osteological differences between the two *Iguana* species, has shown that most of the osteological characteristics used up until now are unreliable. Consequently, a review of the archaeological material using new reliable identification criteria was necessary in order to analyze variations in the taxonomic composition of *Iguana* in archaeological assemblages from the Guadeloupe Islands throughout time. In addition, the reconstruction of the past snout-vent length (SVL) of archaeological *Iguana* (Bochaton, 2016) allows for size comparisons with modern populations.

The aim of this paper is to provide a new analysis of osteological *Iguana* remains from 25 Guadeloupian archaeological sites using new methodological tools developed for the identification (Bochaton et al., 2016b) and zooarchaeological study (Bochaton, 2016) of archaeological *Iguana* remains. These newly obtained zooarchaeological data are then compared with data collected from modern *Iguana* on the Guadeloupe Islands, as well as textual historical data. Finally we use the results to provide evidence of the occurrence of *Iguana* species and morphological changes through time, and describe interactions between past humans and iguanas on the Guadeloupe Islands.

2. Regional setting

The Guadeloupe Islands are situated in the northern Lesser Antilles between Dominica and Montserrat. The archipelago is composed principally of two large islands, Basse Terre (848.1 km²) and Grande-Terre (585.7 km²), separated by a narrow marine channel. Other smaller islands are now clearly separated from the two main islands: La Désirade (21.1 km²) and Îlets de Petite Terre (1.5 km²), Marie-Galante (157.5 km²), and Les Saintes (14.2 km²) (Fig. 1), each with their own geological history. Some of the Guadeloupian islands (Îlets de Petite Terre, Marie-Galante, La Désirade and Grande-Terre) are flat limestone islands, which emerged during the late Calabrian around 800 Ky ago, although La Désirade developed much earlier during the Piacenzian/Gelasian transition at around 2.7 Ma (Bouysse and Guennoc, 1982; Münch et al., 2013). The vegetation of these islands is mainly composed of xerophytic forests and is poorly diversified (Lasserre, 1961). The other islands, Basse Terre and Les Saintes, are volcanic islands which formed between 2.79 and 0.435 My and 4.7 and 0.6 My, respectively (Andreieff et al., 1979; Jacques and Maury, 1988; Samper et al., 2007). Basse Terre is mountainous with many peaks above 1,000 m and a culminating point at 1,467 m (la Soufrière). Pluviometry is higher there than on the other islands and the vegetation is far more diversified with xerophilic, mesophilic, and hydrophilic forests (Lasserre, 1961; Sastre and Breuil, 2007). The morphology and the size of the Guadeloupe Islands varied markedly in relation to sea level fluctuations and the islands of Basse Terre, Grande-Terre, Petite Terre and la Désirade formed a single island during the Late Pleistocene. However, during the chronological period covered by our study (mainly the last two millennia), the morphology of the archipelago was very similar to its current configuration.

As regards past human settlement, the oldest archaeological site of these islands is the site of Morel Zero (Paulet-Locard and Stouvenot, 2005), radiocarbon dated to around 1500 cal. BC

(Mesoindian or Archaic Age), but indirect evidence of human occupation in the form of increased charcoal particles, presumably from human-induced fires, suggests that settlement could have been earlier, ca. 3000 cal. BC. (Siegel et al., 2015; Stouvenot et al., 2014). Morel I on Grande-Terre is the oldest ceramic archaeological site in Guadeloupe Islands dating to around AD 80 and attributed to the Huecan Saladoid culture (Neo-Indian or Early Ceramic Age) (Bérard, 2013; Clerc, 1964; Fitzpatrick, 2015; Hofman et al., 1999; Romon et al., 2006).

This early Saladoid component includes Cedrosan Saladoid ceramic traditions, which occurred between AD 300-900 and evolved into the Marmoran Troumassoid tradition that lasted from AD 900-1500 (i.e., the Late Ceramic Age) (Bonnissent, 2008; Honoré, 2014; Keegan et al., 2013). After Columbus' second trip in 1493 and a period of contact between Amerindian and European populations archaeologically characterized by Cayo complex ceramics, French colonization began around 1635 and led to the disappearance of Amerindian populations (Keegan et al., 2013; Saunders, 2005).

3. Material and Methods

3.1 Zooarchaeological material

The osteological material included in this study comes from 25 pre-Columbian archaeological sites situated on Grande-Terre (5), Basse Terre (7), Les Saintes (1), Îlets de Petite Terre (4), La Désirade (3) and Marie-Galante (5) (Fig. 1; Supplementary material S1; Tab. 1). The chronological or cultural attribution of these sites is reported in Supplementary material S1 and Tab. 1. Most of the sites with the *Iguana* remains studied here had already been investigated by zooarchaeologists who studied the whole bone assemblages recovered in these archaeological deposits (de Waal, 2006; Grouard, 2010, 2007, 2001). For this study, the complete assemblage of

skeletal remains collected from each site was observed in order to review previously identified *Iguana* remains and, when possible, to add newly identified remains. In total, 2,236 archaeological *Iguana* remains were collected from the different assemblages and investigated as part of this study.

3.2 Methodology

Specific identifications followed the osteological characters described by Bochaton et al. (2016b). The latter study is based on a large sample of modern *Iguana* (69 skeletons) and proposes a series of 32 identification criteria distributed among 17 different skeletal (both cranial and postcranial) elements allowing for the distinction of *I. delicatissima*, *I. iguana*, and for some characters, hybrids of the two species. The authors also provided a percentage of reliability for each criterion in order to allow for the discussion of the results. In the present study, archaeological bones that did not present discriminating characters according to Bochaton et al. (2016b) were left specifically unidentified as *Iguana* sp.

The Snout-Vent Length (SVL) estimations of archaeological specimens were obtained using the measurements and predictive equations described by Bochaton (2016) on the different anatomical elements. Skeletal maturity was estimated on the basis of the fully or partially ossified status of each bone and the maturity stages also described by Bochaton (2016). Skeletal maturity and size data were then combined to obtain a “Minimal Theoretical Maximal Size” or MTMS, used to estimate the size that the archaeological specimen would have reached if it had lived until the end of its growth. This MTMS is estimated by considering that the largest immature long bone provides an SVL estimation of a maximum of 80% of the maximal size of the specimen (Bochaton, 2016; Maisano, 2002). Data concerning the size of the modern Guadeloupian *I.*

delicatissima were collected by the French Office National de la Chasse et de la Faune Sauvage (ONCFS) on La Désirade in 2012 (funded by the French state and FEDER) and by the NGO Le Gaiac association on Îlets de Petite Terre (Terre-de-Haut and Terre-de-Bas) between 2007 and 2011, and were made available to us for study.

The minimum number of individuals (MNI) was calculated using the most abundant anatomical element for each site (Shipman, 1981). The global MNI is an addition of the MNI obtained from the different sites considering that it is highly unlikely that a specimen would be divided among different deposits. To study the anatomical distribution of bone remains we used the “Proportional Representation of each skeletal part” (PR) (Dodson and Wexlar, 1979).

Statistical analyses were performed using the free software “R” (version 3.1, <https://cran.r-project.org/>) and “R Studio” (version 0.98.1102). Data normality was tested using the Shapiro-Wilk test. As data were not normally distributed, comparisons between two populations were performed using the Wilcoxon test and comparisons between more than two populations using the Kruskal-Wallis test. Differences were considered to be statistically significant for P value <0.01.

Finally, in order to observe traces hypothetically left by humans on *Iguana* bones, all the remains were carefully observed using a stereomicroscope (Nikon SMZ1000). In addition, Scanning Electron Microscope (SEM) photographs of digested bones were taken.

4. Results

4.1 Specific identification (Figure 2; Tab. 1)

199 A total of 2,236 *Iguana* remains (MNI=80) were collected from the different archaeological sites
200 studied here. Among these remains, 1,826 (81.7%) did not present any of the anatomical
201 structures taken into account by Bochaton et al. (2016b) and thus could not be identified at the
202 species level. The other 410 remains were identified at the species level. They nearly all (407
203 remains-18.2%) presented the following *I. delicatissima* characteristics that differ from *I. iguana*
204 (see Bochaton et al., 2016b): On the maxilla, the infraorbital foramen is more anteriorly located
205 on the supradental shelf than on *I. iguana* and can reach the transversal crest, and the exonarinal
206 margin of the facial process forms an obtuse angle with the premaxillary process in lateral view;
207 On the frontal bone (Fig. 2), the smallest width of the interorbital constriction is superior to 50%
208 of the maximal lateral length of the bone, the posterolateral processes are oriented
209 posterolaterally and articular facets with the parietal are oriented dorsally and are clearly visible
210 in dorsal view, and the bone presents a posterior braincase depression in ventral view; On the
211 parietal bone (Fig. 2), the pineal foramen is not well delimited on the frontal margin of the bone
212 and articular facets with the frontal bone are oriented ventrally and highly visible in ventral view;
213 On the postorbital bone, the postorbital articular facet with the jugal is medially directed and
214 more visible in medial view than in *I. iguana*, and the articular facets with the jugal and
215 squamosal form two individualized facets; On the jugal bone, the dorsal view of the jugal
216 suborbital ramus bears a well-developed anteromedial expansion between the palatine and
217 ectopterygoid insertion regions; On the pterygoid bone, only one weakly posteriorly extended
218 dental row occurs, and the lateral area of the bone is flat; On the sphenoid bone, the sphenoid
219 ventral crests joining the basal tubercle to the basiptyergoid is sigmoid in ventral view; On the
220 dentary, the intramandibular lamella is short and expands below the first to second dental
221 positions; On the coronoid bone, the coronoid process is higher and more dorsally rounded in
222 lateral view than in *I. iguana*, this process may also present a small posterior protuberance; On

the articular bone, the length of the retroarticular process is inferior to 150% of the length of the articular fossa and the tympanic crest is wider than the angular crest; On the surangular bone (Fig. 2), the surangular coronoid process is pointed; On the axis vertebra, the ratio between the minimal neural arch length and the posterior neural arch breadth comprising the postzygapophysis is inferior to 0.65; All the caudal vertebrae lack caudal autotomy planes; On the scapulocoracoid bone, the small posterolateral protuberance marking the attachment of the scapulohumeral ligament is absent; On the pelvic bone, the ilium dorsal crest is convex and bears a short and curved ventral edge, the posterior section of the ilium is subtriangular, the anterior section of the pubis forms a triangle with an acute apex angle, and the posterior margin of ischium is more concave than in *I. iguana*; On the humerus (Fig. 2), the foramen of the supracondylar fossa is more open than in *I. iguana*.

However, three remains (0.1%) presented the following *Iguana iguana* characteristics: an infraorbital foramen posteriorly located on a maxilla, and an exonarinal margin of the facial process forming a right angle with the premaxillary process in lateral view on the same bone; an intramandibular lamella anteriorly extended under the four last dental positions on a dentary, and a narrow foramen of the supracondylar fossa on a humerus.

4.2 Body size characteristics of *Iguana* archaeological populations

Past Snout-Vent Length (SVL) and skeletal maturity were observed on all the studied *Iguana* remains. Past Snout-Vent Length (SVL) estimations were obtained from 488 *Iguana* remains (MNI=48) from all skeletal parts for which size predictive equations were defined by Bochaton (2016). These remains come from all of the archaeological sites included in this study and a list of all the obtained estimations can be found in Supplementary material (S2).

The estimated size ranged from around 70 mm SVL for small newborn specimens to very large individuals with SVL of more than 500 mm (Fig. 3, Supplementary material S2). However, all size classes were not equally distributed in our assemblage. Specimens smaller than 220 mm SVL were nearly absent and most fossil *Iguana* had a SVL between 300 and 400 mm. Specimens smaller than 220 mm SVL (between 70 and 150 mm SVL) only occur in Morne-Rita on Marie-Galante Island (NMI=1), Cathédrale de Basse-Terre on Basse Terre Island (NMI=1) and Anse à la Gourde on Grande-Terre Island (NMI=2) (Fig. 3, Supplementary material S2).

Skeletal maturity data (bone ossification) were recorded on 223 archaeological *Iguana* remains. Among them, 65 (29%) were mature bones of which 35 belong to fully-grown specimens (with fully ossified long bones and/or fused sacral vertebrae = stage 4 *sensu* Bochaton, 2016). The other 158 remains (71%) correspond to non-fully grown individuals and at least 13 of them belong to non-sexually mature specimens (for which the pelvic girdle and axis are not fully ossified = stage 2 *sensu* Bochaton, 2016).

Moreover, 114 remains yield a combination of both size and skeletal maturity data and thus allow for the estimation of the MTMS and the size range of the previously defined maturity stages. The detailed observation of archaeological *Iguana* sizes was performed at the island scale because the material was too scant to obtain significant results for each site. In addition, we noted that archaeological specimens collected from the different Guadeloupe islands present SVL differences (Kruskal-Wallis test, $p.val < 0.01$) (Fig. 3). Size overlap often occurred between the defined maturity stages. This could reflect a size estimation error linked to measurement error, variability in bone maturation timing or could also be the result of sexual size dimorphism.

On Marie-Galante, the Minimal Theoretical Maximal Size (MTMS) of archaeological *Iguana* was 475 mm, and the estimated SVL mean was 324 mm (Fig. 3-A). A size overlap of a maximum of 40 mm was observed between the maturity stages. The results were similar for the sites from Îlets de Petite Terre (Fig. 3-B), La Désirade (Fig. 3-C), and Grande-Terre (Fig. 3-D): MTMS are respectively 462, 460 and 475 mm with mean estimated SVL of 330, 358 and 310 mm respectively. On Îlets de Petite Terre and Grande-Terre, some limited size overlap (between 19 and 25 mm) was observed between maturity stages. A single archaeological SVL datum (361 mm) was collected from Les Saintes Island.

The situation was more complex for archaeological *Iguana* from Basse Terre Island, as two groups of very different sizes seem to occur in the same archaeological contexts. Most of the specimens are larger than any other observed specimens, with estimated sizes between 400-450 mm SVL for non-fully mature bones (MNI=1), reaching a maximum of 511 mm SVL for fully mature bones (MNI=2) (Fig 3-E). However, some specimens (MNI=2) present estimated sizes of only 323 and 388 mm SVL for fully mature bones. This situation led to an important body size overlap between maturity stages and made the definition of a single MTMS impossible. Consequently, we defined two MTMS on the basis of the smallest mature and largest immature bones and obtained MTMS of respectively 403 mm and 556 mm SVL (Fig. 3-E). These two MTMS correspond to two populations presenting different body sizes. Taken as a whole, the estimated SVL of Basse Terre archaeological iguanas (mean= 364 mm) were the highest for the archipelago.

We did not observe any effects of chronological attribution (Saladoid or Troumassoid) on the size of the *Iguana* remains (Wilcoxon test, $p.val=0.34$). However, comparisons of SVL data collected from modern *I. delicatissima* populations from La Désirade ($n= 274$) and Îlets de Petite Terre

(Terre-de-Haut and Terre-de-Bas) (n=435) with all archaeological SVL data obtained from these islands show that archaeological iguanas were far larger than modern specimens (Wilcoxon test, p.val <0.001). Indeed, modern iguanas from three islands do not exceed 390 mm SVL (max. 390 mm on Terre-de-Haut [see also Breuil, 2002], 385 mm on Terre-de-Bas and 360 mm on La Désirade [387 mm following Schardt, 1998]), whereas archaeological iguanas from the same islands can be larger than 450 mm SVL. The SVL mean of archaeological iguanas (330-358 mm) was also higher than the SVL mean of modern iguanas (258-274 mm), but as the specimens occurring in archaeological sites and measured in the field are probably subject to very different sampling methods, SVL means are nearly impossible to interpret. A very dry season in 2001 led to high mortality among iguanas from La Désirade and Petite-Terre islands (Breuil, 2002) and could have contributed to the elimination of large specimens. However, archaeological iguanas from these islands are still larger than any modern *I. delicatissima* ever measured in the Lesser Antilles, and a reduction in size during the modern period is very likely.

4.3 Skeletal distribution, anthropic marks, and surface alterations of the archaeological remains

Due to the scarcity of *Iguana* remains in archaeological sites, we did not find clear site-scale differences in the data presented in this section. Consequently, all the sites were treated as a whole, but unusual observations encountered at single sites are also mentioned when pertinent.

The overall representation of skeletal parts was low (PR=12.5%), which means that on average only 12% of *Iguana* skeletons were present in the archaeological sites, but all the anatomical parts were represented. The most represented anatomical parts are the proximal part of the tail (PR=42), femur (PR=32), humerus (PR= 29), middle part of the tail (PR=28), pelvic girdle (PR=25), dorsal vertebrae (PR=24), and tibia (PR=22) (Fig. 4). These anatomical parts are the

311 most important in terms of meat content, especially the proximal part of the tail, the humerus, and
312 the femur. However, these bones are also the biggest and strongest elements, and are the most
313 likely to be preserved and collected. All the other bones, although less represented, were also
314 present in the assemblages (Fig. 4). These bones are smaller elements, sometimes fragile and
315 subject to high breakage rates, and are thus more exposed to collection bias, especially
316 considering that 80% of the studied bones were broken.

317 Traces of burning, cut marks and digestion marks were rare on the examined material and only
318 occurred on 84 remains (3.7% of the total assemblage). Most of the observed traces (56) were
319 traces of fire, ranging from black burning marks (Stages 1 and 2 from Stiner and Kuhn 1995;
320 N=45) to white calcination marks (Stages 4 and 5 from Stiner and Kuhn 1995; N=11). These
321 marks indicate that bones presenting black marks were exposed to temperatures superior to 300
322 °C and those presenting white marks to 675 °C (Munro et al., 2008). These traces of fire occur
323 mostly on skeletal extremities: caudal vertebrae (N=21), the phalanx (N=8) and cranium (N=6)
324 (Fig. 4, 5). Cut marks were also observed on 16 remains (Fig. 4, 5), but were difficult to observe
325 because of bone alterations such as the occurrence of concretions or surface degradation. These
326 marks only occurred on long bones (N=5), the pelvic girdle (N=3) and vertebrae (N=8) (Fig. 4).
327 The most recurring location of cut marks was on mid-caudal vertebrae (N=6), where traces
328 occurred all around the vertebrae and clearly reflected the removal of the distal part of the tail,
329 which is very long and poor in meat. Cut marks observed on this area were sometimes combined
330 with traces of fire (Fig. 5). Digestive marks were also observed on 12 remains, but only attributed
331 to small specimens with SVL of around 90 mm, at Anse à la Gourde and in cave deposits (Anse à
332 l'Ecu, Morne-Rita and Cadet 3). We considered some of these bones to be highly digested, as
333 shown by two dentaries (Fig. 6) displaying surface dissolution, enlargement of labial foramina

(Fig. 6-A), and the destruction of most of their teeth. Such traces were probably left by humans, carnivores, or diurnal raptors (Andrews, 1990; Stoetzel et al., 2012).

5. Discussion

5.1 Taxonomic identification of archaeological iguanas

Among the 410 archaeological remains identified to the species level, 407 were attributed to *I. delicatissima* and only three to *I. iguana*. However, these *I. iguana* identifications are highly uncertain. Indeed, two of them (a maxilla and a humerus from the Basse-Terre Gare Maritime site) were identified using characteristics that are not considered to be 100% reliable (Bochaton et al., 2016b). They could represent misidentifications in view of the large number of studied archaeological remains. The third bone presenting an *Iguana iguana* characteristic is a dentary from the Tourlourous site on Marie-Galante. It was identified based on a 100% reliable character (character I from Bochaton et al., 2016b). However, this attribution is still dubious as the bone is very isolated in an assemblage where 99.7% of the remains were unambiguously attributed to *I. delicatissima*. Given this context, a single remain bearing an *I. iguana* character is clearly insufficient to consider the occurrence of that species at the Tourlourous site. The most likely explanation is that the diagnostic characteristic described for the dentary by Bochaton et al., 2016b is not 100% reliable. This would not be surprising considering the important skeletal morphological overlap between *I. iguana* and *I. delicatissima* described by previous authors and the limited number of available comparative specimens. Consequently, *I. delicatissima* seems to be the only *Iguana* species occurring on the Guadeloupe Islands during pre-Columbian times and there is no clear evidence of the occurrence of *I. iguana* during that period. In addition, the extreme scarcity of *I. iguana* elements in our material shows that these *I. delicatissima*

populations bear no traces of past hybridization with *I. iguana*. These results differ from those obtained by Martin (2009) and Martin et al. (2010), who stated that both *I. iguana* and *I. delicatissima* occurred prehistorically on the Guadeloupe Islands. This contradiction is undoubtedly due to the unreliability of the identification characters used by these authors (Bochaton et al., 2016b).

Consequently, previous results should no longer be taken into account and we should currently consider that there is no evidence of past occurrences of *I. iguana* on the Guadeloupe Islands prior to European contact. This conclusion can be related to the long-standing discussion concerning the introduced or native status of *I. iguana* in the Lesser Antilles. The introduced status of *I. iguana* was first suggested by Dunn (1934) and then Underwood (1962), but subsequently refuted by Lazell (1973). Later, Lescure (1983) suggested an Amerindian role in the dispersal of *I. iguana* in the Antilles and more recently Breuil (2013, 2002), Breuil et al. (2010) and Vuillaume et al. (2015) assumed that *I. iguana* was introduced to the Guadeloupe Islands and St Maarten during the 19th and 20th centuries. Our results concur with the latter hypothesis and should contribute to addressing this long-standing debate.

5.2 Size of past iguanas

Moreover, we investigated the past size of *I. delicatissima* in the Guadeloupe Islands for the first time. In order to achieve this, we observed two estimated size variables; the mean SVL and Minimal Theoretical Maximal Size (MTMS) of past iguanas from each island and found that these variables showed conflicting results. Indeed, although both variables showed inter-island differences, the mean SVL indicated that past iguanas were larger on Basse Terre and La Désirade than on Marie-Galante and Îlets de Petite Terre (Terre-de-Bas), and even smaller on

Grande-Terre (Fig.3). Conversely, the MTMS (between 460 and 475 mm SVL) indicated that iguanas were of similar size on all the islands with the exception of Basse Terre, where they were larger (Fig.3). The advantage of the MTMS value is that it also takes account of the skeletal maturity of past iguanas and not simply their size. Thus, it allows for the study of the body size of archaeological populations of consumed animals, with often strongly biased size composition: we clearly demonstrated a size selection by human hunters on the studied archaeological iguanas (see below). Thus we consider the mean body size differences observed on archaeological iguanas from the different islands as a bias induced by differential sampling selection by past humans rather than true biological differences.

Consequently, we assume that the past size of *I. delicatissima* was similar on Marie-Galante, Îlets de Petite Terre (Terre-de-bas), La Désirade and Grande-Terre. However, larger iguanas occurred on Basse Terre Island, as shown by the MTMS (superior to 550 mm). The larger sizes observed on that island could be linked to indirect geographic and environmental effects. On account of its volcanic nature, Basse Terre is more humid and presents more mountainous zones and habitat diversity than the limestone islands (Lasserre, 1961; Lescure, 1987). It is also noteworthy that the biggest modern *I. delicatissima* ever measured on Guadeloupe Islands (410 mm SVL) originated from that island (Breuil, 2002). However, smaller archaeological specimens (MTMS= 403 mm) were also recovered from Basse Terre. Size differences between these small and large iguanas occurring on Basse Terre are far too high to be related to the same sexual dimorphism as in modern *I. delicatissima*, which does not appear to be as marked according to the ONCFS data collected on La Désirade and Petite Terre (a difference of 20 mm in SVL between the largest measured female and male) and to data collected on Dominica (a difference of 42 mm in SVL between the largest measured female and male) (Knapp et al., 2016), or to a size estimation error.

It is possible that sexual dimorphism may have been more marked in Basse Terre iguanas than in modern iguanas but genetic or isotopic data would be needed to confirm this hypothesis. Another alternative explanation is that these small iguanas could correspond either to an isolated local population subject to unfavorable biotic and/or abiotic conditions or exogenous iguanas translocated by pre-Columbians from another island.

5.3 Pre-Columbian population interactions with iguanas

The similarity in size of *I. delicatissima* indicated by the MTMS on most islands, including Marie-Galante (Fig. 3), where they were probably introduced (Bochaton et al., 2015), could also point to their introduction to other islands (see also Vuillaume et al., 2015), possibly by human populations, probably for feeding purposes. However, this hypothesis lacks theoretical grounds considering that island size only has a slight effect on squamate body size (Meiri, 2007) and this similarity in size could also be the consequence of convergent evolution. The occurrence of *Iguana delicatissima* remains in most of the Guadeloupian pre-Columbian archaeological sites indicates that these large lizards were collected by human pre-Columbian populations for two thousand years (from 500 BC to AD 1500), possibly using specific hunting strategies. Indeed, hunted iguanas were not randomly selected, as suggested by archaeological *Iguana* size distribution, which does not reflect natural population size ranges. Most of the archaeological assemblages exclusively include large iguanas (mainly between 300 and 400 mm SVL) and young individuals (with SVL of less than 180 mm) are largely absent from archaeological deposits (Fig. 3). Although archaeological collection methods (for instance, the use of sieves and mesh size) could influence the observed size distribution, they cannot account for the lack of medium-sized individuals, as smaller taxa occur at all of the investigated sites. Thus, the observed distribution is likely to reflect human selection of the largest animals, which provide the

most meat, and points to the difficulties involved in catching young iguanas or to the lack of interest they present in terms of meat intake. However, this size selection seems to differ between islands. Indeed, the difference between the MTMS of iguanas from each island and the average size observed in the archaeological sites of the same island differs among islands. These differences can be interpreted in terms of selection intensity: lower differences between the mean size and the MTMS point to the more marked selection of large specimens. This difference is especially low on La Désirade and Îlets de Petite Terre (102-132 mm), where selection seems to be strongest. However, it is higher in Marie-Galante and Grande-Terre (151-165 mm), and even higher in Basse Terre (192 mm), where selection appears to be low. The strong selection of large specimens on La Désirade and Îlets de Petite Terre could reflect the high density of *Iguana* populations, and thus the wide choice available to hunters, whereas conversely, population density would have been lower on Marie-Galante and Grande-Terre. The results from Basse Terre, indicating populations of different body-size, were difficult to assess. In the light of these data it is interesting to observe that Îlets de Petite Terre and La Désirade are the only islands in Guadeloupe still inhabited by large populations of *I. delicatissima* (Breuil, 2002). This could perhaps be explained by their isolation and high population density, preserving them from extirpation.

This clear size selection applied to archaeological specimens reflects the hunter's capacity to select hunted specimens and thus indicates the use of specific hunting techniques. No evidence of injuries was observed on these bones, but historical sources from European authors describing mid-17th century Amerindians provide useful information about how pre-Columbian iguanas may have been hunted. These authors indicated that iguanas were caught by Carib Indians using a simple noose mounted on a perch that was discreetly passed around the iguanas' necks

447 (Rochefort, 1658; Du Tertre, 1667; Maurile de Saint Michel (ca 1615-1669) in Grunberg, 2013).
448 The same technique was still used by Guadeloupe and La Martinique inhabitants long after the
449 disappearance of pre-Columbian hunters (Labat, 1724; Pinchon, 1971). After being caught, the
450 authors also explained that the animals were carried to the site and kept alive, sometimes for
451 several weeks (Du Tertre, 1667; Grunberg, 2013b; Rochefort, 1658), as suggested by the
452 occurrence of all the anatomical pieces in the bone remains from the sites (Fig. 4). But iguanas
453 were also cooked, as shown by the rare traces of fire and cut marks observed on archaeological
454 remains, which can also be correlated to historical literature sources. Indeed, the anonymous
455 author from Carpentras who described 17th century Amerindians, explained that after being
456 brought back to the village, the iguanas were burned to kill them and remove their skin before
457 being dismembered (Anonyme de Carpentras (1618-1620) in Grunberg, 2013b). We observed
458 rare fire marks on *Iguana* bones on the thinnest anatomical parts most exposed to fire (skull and
459 extremities including sectioned tails). These marks could reflect the burning practices described
460 by the anonymous Carpentras author (Anonyme de Carpentras (1618-1620) in Grunberg, 2013b).
461 The rarity of such marks could also correspond to the practice of boiling described by the same
462 author (Anonyme de Carpentras (1618-1620) in Grunberg, 2013b), or to drying or smoking the
463 carcass, as often practiced by Amerindian populations. However, there is no mention of removing
464 the tail; a practice clearly established on archaeological iguanas and observed by one of us (S.
465 G.), along with the removal of the skin and extremities of the carcass just before cooking.

466 The rare digestion traces observed on archaeological remains are intense, easily visible, and only
467 occur on small specimens, highlighting the particularity of these small remains, which clearly
468 differ from the main size distribution. These remains could reflect the occasional human
469 consumption of young iguanas but such small animals may also have been eaten by non-human

predators. Thus, for the digested remains found at the open-air archaeological sites in Anse à la Gourde, one of the most plausible hypotheses would be that these small iguanas were hunted by domestic dogs, since dogs occur in archaeological sites and were part of the daily life of pre-Columbian populations in the Guadeloupe Islands (Grouard, 2001; Grouard et al., 2013). Alternatively, some of the remains collected in cave deposits (Anse à l'Ecu, Morne-Rita and Cadet 3) may reflect predation by birds of prey.

5.4 Size evolution of *Iguana delicatissima* over time

Several hundreds of years of pre-Columbian hunting do not seem to have impacted *I. delicatissima* populations, in contrast to the activities of modern human populations. Indeed, according to archaeological evidence, the size of iguanas seems to remain stable throughout the pre-Columbian period. Conversely, comparisons with modern data collected on Îlets de Petite Terre (Terre-de-Haut and Terre-de-Bas) and La Désirade, the only two islands in Guadeloupe still densely inhabited by *I. delicatissima*, show a possible significant decrease in size between pre-Columbian and modern times, estimated at about 20% of *I. delicatissima* SVL size. In addition, no present-day *I. delicatissima* equivalent in size to the largest archaeological iguanas has ever been measured, since the highest SVL ever recorded on a *I. delicatissima* specimen is only 430 mm SVL (from Dominica; Day et al., 2000), as opposed to a maximum of 550 mm SVL for the largest archaeological specimen. As a precaution we should nevertheless note that it is difficult to assess the reliability of extreme archaeological SVL values, especially for the largest archaeological specimens with a SVL of more than 500 mm. This is because such sizes exceed the size of the modern specimens used by Bochaton (2016) to construct SVL estimation equations. However, such very high sizes are close to the size of the iguanas described by Du

Tertre in Guadeloupe during the 17th century, when a total length of 160 cm corresponds to an SVL of around 53 cm (Du Tertre, 1667).

However, although no equivalent sized *I. delicatissima* has ever been measured or collected, this does not mean that it never existed. Indeed, Lazell (1973) mentioned that the small size of *I. delicatissima* in museum specimens could be due to sampling bias. He also claimed that he saw large specimens in Les Saintes and Dominica, with an SVL of around 400-450 mm, an observation confirmed on Dominica where the largest modern iguanas attain a maximal SVL size of 428 mm (Knapp et al., 2016). Still, even if the accuracy of estimated past iguana size is difficult to assess, a significant decrease in the size of this lizard on the Guadeloupe Islands over the past few centuries seems likely. As a consequence, the decrease in squamate size during the Holocene previously highlighted by Pregill (1986) in other West-Indian squamates also seems to apply to *I. delicatissima* from the Guadeloupe Islands. This constitutes further evidence of the strong impact of human populations after the European colonization of these islands, where *I. delicatissima* populations were well established and healthy, as suggested by their large size, despite extensive exploitation by pre-Columbian hunters. These results differ from those obtained by Carlson and Keegan (2004) on Grand Turk Island (Greater Antilles), where pre-Columbian hunting seemed to result in a size diminution in rock iguanas, probably on account of over-exploitation on a relatively small island (only 18 km²). But this phenomenon concerns pre-ceramic populations relying largely on terrestrial fauna for food sources (40% of the MNI of the Grand Turk Island site corresponds to iguanas). Conversely, the archaeological sites concerned by our study concern more recent ceramic cultures that rely mainly on marine resources and squamate remains represent a very minor part of the osteological assemblages (below 6% and often less than 1% of the vertebrate remains collected in each site [de Waal, 2006; Grouard, 2010,

2007, 2001; Bochaton, work in progress]). Up until now, few data were available concerning the pre-ceramic cultures and their subsistence strategies on the Guadeloupe Islands, and iguanas from these periods, as well as from pre-anthropoc periods, remain unknown to us.

6. Conclusion

Our data clearly show that populations of *Iguana delicatissima*, were formerly present on all of the Guadeloupe Islands during pre-Columbian times and that at the same period, the invasive species, *I. iguana* was absent, confirming that it was introduced to this archipelago during the past few centuries. Iguanas were the object of selection focusing on large specimens by pre-Columbian hunters, as attested by the size reconstruction of archaeological specimens. The meat from these lizards was cooked and consumed by Amerindians, as described in historical sources recounting the daily life of 17th century Caribbean Amerindians. Hunting by pre-Columbian hunters had no visible effect on past iguana populations. However, comparisons with modern data demonstrate that *I. delicatissima* is now extinct on most of the Guadeloupe Islands and is 20% smaller on the islands where it still occurs. This fact highlights the massive impact of European and historical populations on these large lizards, which mostly became extinct or underwent a drastic decrease in body size over the past three centuries. Such phenomena impacting iguanas were also observed using archaeological or subfossil data for several other taxa in the Caribbean (MacPhee, 2009; Steadman et al., 2015; Stoetzel et al., 2016) and in other geographic areas (Grayson, 2001; Nakamura et al., 2013; Steadman, 1995). They provide further evidence of the strong impact of modern societies on fauna in the context of the current biodiversity crisis (Barnosky et al., 2011; Burney and Flannery, 2005; Ceballos et al., 2015).

Similar studies to ours would allow for the observation of past hitherto hidden or inaccurately recorded phenomena, such as the timing of colonization, spatio-temporal morphological changes throughout time or the natural or human-mediated introduction of exogenous species. They would also lead to the testing of several hypotheses based on modern data. However, with regard to archaeological lizards and snakes, such studies are extremely rare (de Buffrénil and Hemery, 2007; Klemens and Thorbjarnarson, 1995; Monchot et al., 2014) and much work remains to be done in order to elucidate recent squamate history and interactions of these animals with past human populations all over the world.

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Island	Site	Date	<i>Iguana delicatissima</i>	<i>Iguana iguana</i>	<i>Iguana</i> sp.	NR tot.	MNI
Basse-Terre	24, rue Schoelcher	Early Saladoid	2	0	2	4	1
	Cathédrale de Basse-Terre	Early Saladoid	31	0	122	153	6
	Embouchure de la Rivière Baillif	Late Saladoid	0	0	1	1	1
	Gare Maritime	Early Saladoid	143	2	361	506	14
	Grande-Anse Trois Rivières	Late Troumassoid	0	0	1	1	1
	Place Saint-François	Early Saladoid	0	0	1	1	1
	Sainte-Rose La Ramée	Early Troumassoid	19	0	166	185	4
	Total island		195	2	654	851	28
Grande-Terre	Anse à la Gourde	Late Saladoid-Late Troumassoid	36	0	388	424	8
	Anse à l'Eau	Late Saladoid	6	0	18	24	3
	Grotte de l'Anse à l'Ecu	Modern	0	0	1	1	1
	Grotte de l'Anse à la Gourde	Modern	1	0	4	5	1
	Morel	Early Saladoid – Troumassoid	5	0	49	54	4
	Total island		48	0	460	508	17
La Désirade	A l'Escalier	Troumassoid	2	0	19	21	1
	Petite Rivière	Late Saladoid –Early	10	0	132	142	7
	Pointe Gros Rempart 6	Modern	0	0	2	2	1
	Total island		12	0	153	165	9
Petite-Terre	Baleine Sud	Troumassoid	2	0	10	12	1
	Caille à Bélasse	Late Troumassoid	77	0	201	278	4
	Mouton de Bas	Troumassoid	5	0	20	25	1
	Site du phare	Troumassoid	0	0	4	4	1
	Total island		84	0	235	319	7
Marie-Galante	Grotte Blanchard	Late Troumassoid	3	0	4	7	1
	Abri Cadet 3	Archaic, Late Troumassoid	1	0	0	1	1
	Folle Anse	Early Saladoid-Troumassoid	1	0	4	5	1
	Grotte du Morne Rita	Archaic-Saladoid	0	0	2	2	1
	Tourlourous - Stade José Bade	Late Saladoid-Early and Late	63	1	312	376	14
	Total island		68	1	322	391	18
Les Saintes	Grande-Anse de Terre de Bas des Saintes	Late Troumassoid	0	0	2	2	1
	Total island		0	0	2	2	1
	Total		407	3	1826	2236	80

Table 1: Number of *Iguana* remains (NR) collected from each archaeological site along with their attribution to *I. delicatissima*, *I. iguana* or *Iguana* sp. and Minimal Number of Individuals (MNI). Cultural attribution of each deposit is also indicated: Archaic= 2000 - 500 BC, Saladoid = AD 80 - 900, Troumassoid = AD 900 - 1490, Modern=1493 – present.

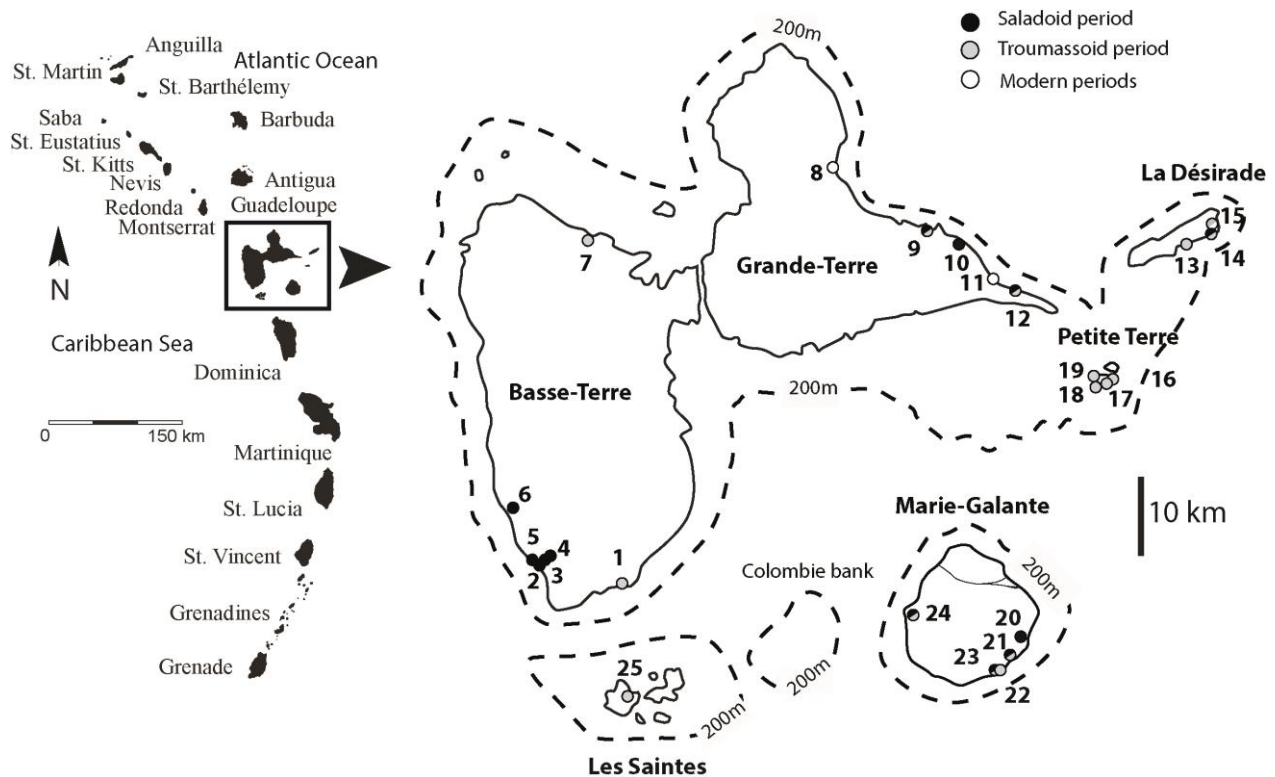
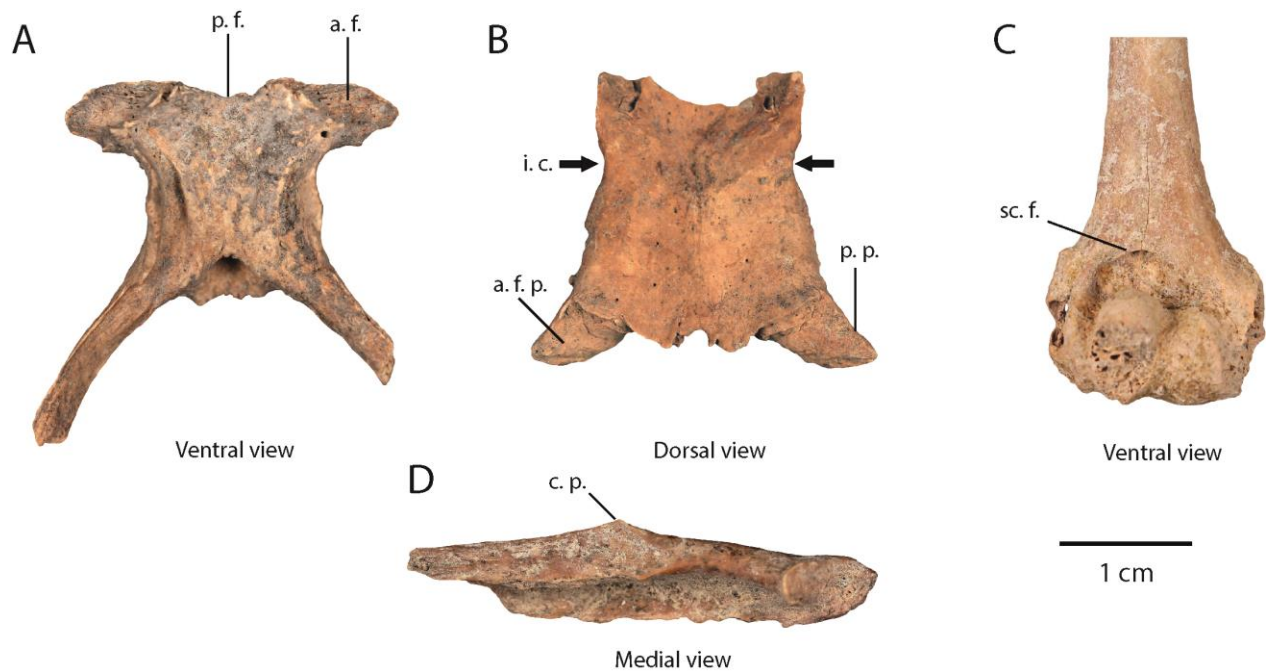


Figure 1: Map of the Lesser Antilles and focus on the Guadeloupe Islands with isobaths (-200m) from Münch et al. (2013) and location of the studied archaeological sites with their chronological attributions (Saladoid period (AD 80 - 900), Troumassoid period (AD 900 - 1500) or Modern period (AD 1493 – present): 1: Grande-Anse Trois Rivières; 2: 24, rue Schoelcher; 3: Place Saint-François; 4: Cathédrale de Basse-Terre; 5: Gare Maritime de Basse-Terre; 6: Embouchure de la Rivière Baillif; 7: Sainte-Rose La Ramée; 8: Grotte de l'Anse à l'Ecu; 9: Morel; 10: Anse à l'Eau; 11: Grotte de l'Anse à la Gourde; 12: Anse à la Gourde; 13: A l'Escalier; 14: Petite Rivière; 15: Pointe Gros Rempart; 16: Site du phare; 17: Baleine Sud; 18: Caille à Bélasse; 19: Mouton

795 de Bas; 20: Grotte du Morne Rita; 21: Tourlourous - Stade José Bade; 22: Grotte Blanchard; 23:
796 Abri Cadet 3; 24: Folle Anse; 25: Grande-Anse de Terre de Bas des Saintes.



797
798 Figure 2: Examples of *Iguana* bone remains from the Gare Maritime site (Basse Terre),
799 presenting the *I. delicatissima* characters described by Bochaton et al., (2016b): A) Parietal with
800 an inconspicuous pineal foramen (p. f.) and two clearly visible articular facets with the frontal (a.
801 f.) in ventral view (US1008); B) Frontal with weak interorbital constriction (i.c.), posterolaterally
802 oriented posterior processes (p. p.) and articular facet with the dorsally oriented parietal (a.f.p.)
803 (US1008); C) Humerus with foramen of the supracondylar fossa (sc. f.) largely open (US1008);
804 D) Surangular with pointed coronoid process (c. p.) (US1011).

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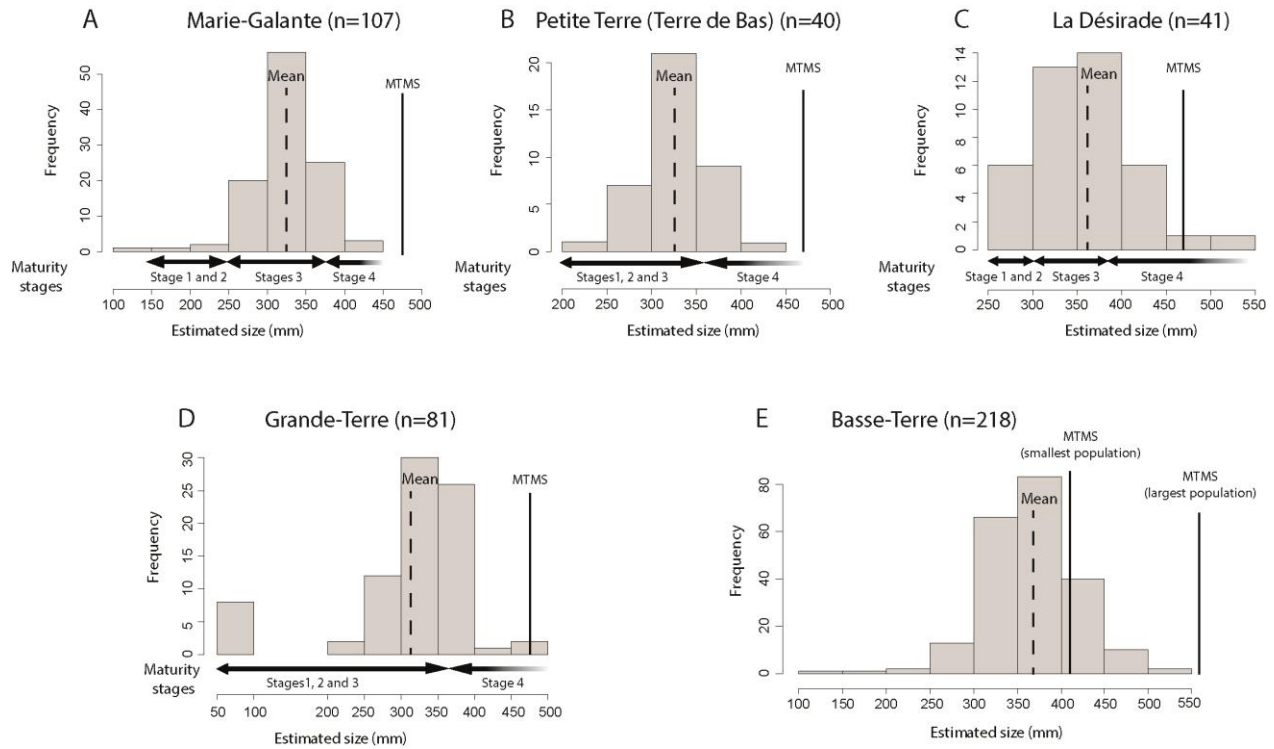


Figure 3: Distribution of estimated SVL size (in millimeters) obtained on archaeological *Iguana* remains from A: Marie-Galante, B: Îlets de Petite Terre, C: La Désirade, D: Grande-Terre and E: Basse Terre islands. The Minimal Theoretical Maximal Size (MTMS) is provided for each island along with the correspondence between size and skeletal maturity stages defined by Bochaton (2016).

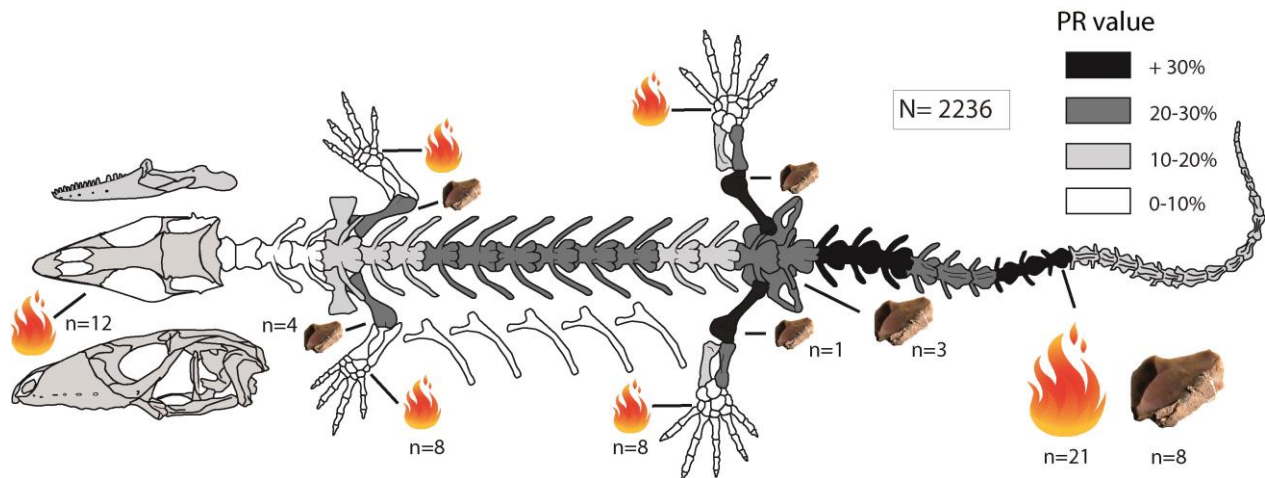


Figure 4: Anatomical distribution of *Iguana* remains from the 25 sites with PR value (Dodson and Wexlar 1989) for each anatomical part along with the occurrence of fire traces (fire symbol) and cut marks (modern flint tool symbol) on the extremities of the skeleton (skeleton drawing modified from Coutureau, 2004).

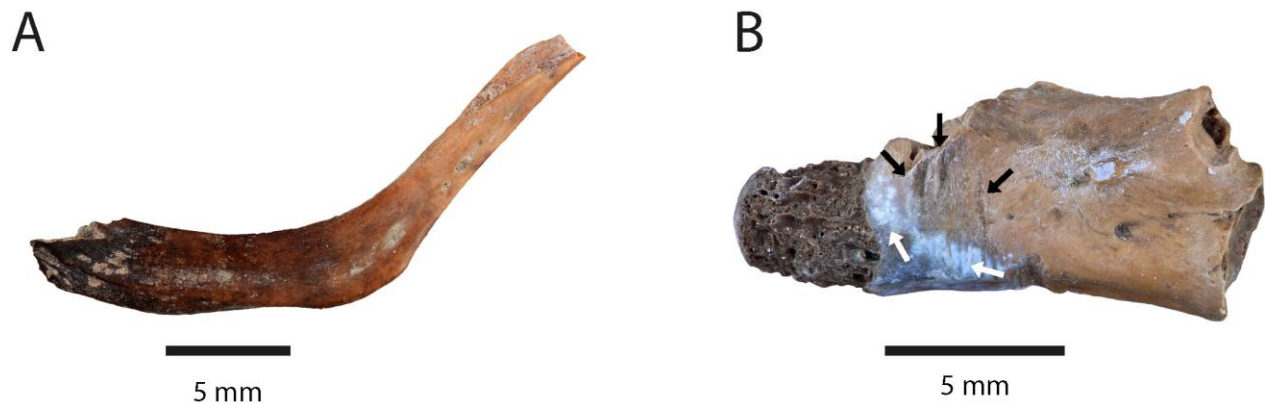
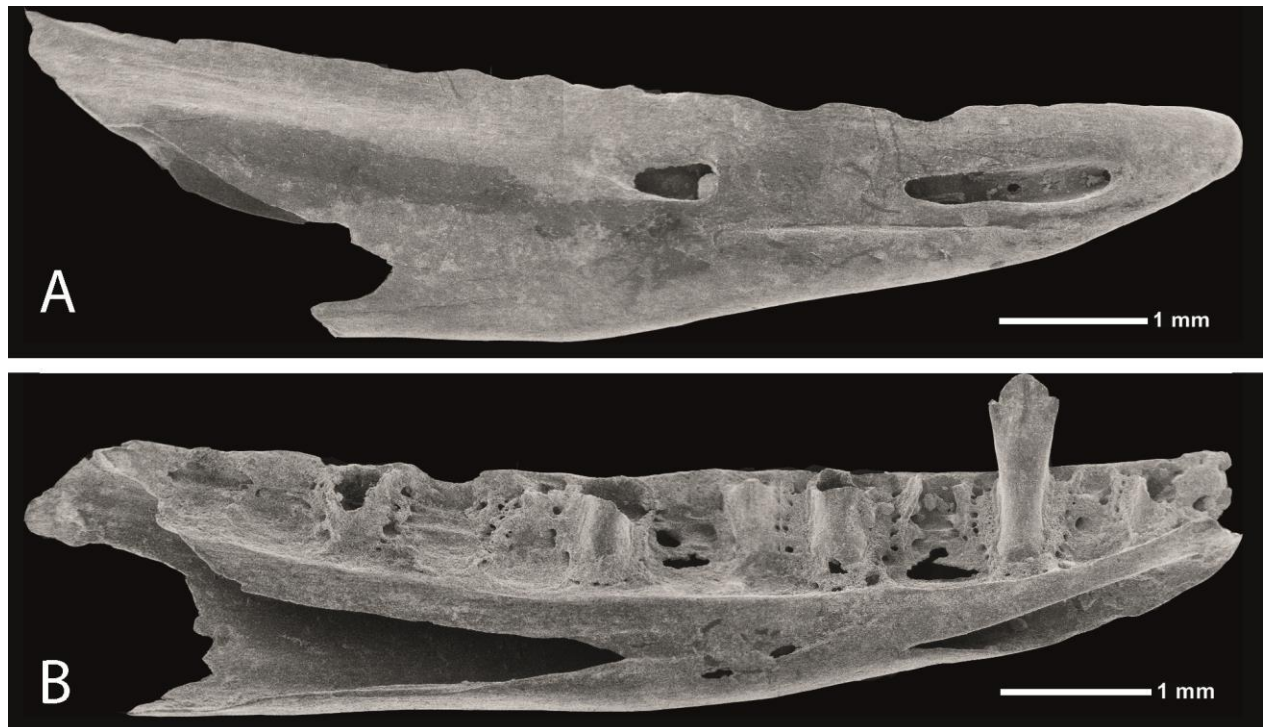


Figure 5: A) Half-burnt (black) left jugal bone of *I. delicatissima* from Caille à Bélasse site (Square O51c – dec11). B) Caudal vertebra of *I. delicatissima* in lateral view with white burning

824 traces (white arrows) and cut marks (black arrows) showing the removal of the tail from Anse à
825 la Gourde site (year 1997- Z64 S93 C1 lvl 4).

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829 Figure 6: SEM pictures of digested dentaries of young *I. delicatissima* from Anse à la Gourde site
830 (Year 1995-US6): A) labial view of a right dentary; B) lingual view of a left dentary.