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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4   Running title: Past *Iguana* from the Guadeloupe Islands

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16

17   Abstract

18   Among the lizards in the Lesser Antillean Islands, iguanas are undoubtedly the most emblematic,

19   especially the endemic species, *Iguana delicatissima*. However, although much effort is currently

20   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

44 et al., 2016; Grouard, 2001; Stouvenot et al., 2014) show that most of the past endemic squamates

45 of these islands have become extinct, mainly during the recent past.

46 The most emblematic of the surviving reptiles is probably the genus *Iguana* Laurenti, 1768,

47 represented by the green iguana (*Iguana iguana* [Linnaeus, 1758]), and the Lesser Antillean

48 iguana (*Iguana delicatissima* Laurenti, 1768) (Breuil, 2002; Henderson and Breuil, 2012). These

49 two species diverged around 22.8 Mya ago (Hedges et al., 2015) and are both present in the

50 Lesser Antilles. However, they seem to have undergone different local evolutionary histories,

51 although they can still breed together and produce fertile offspring (Vuillaume et al., 2015). *I.*

52 *iguana* has a very broad natural distribution area in continental Central and South America

53 (Stephen et al., 2013) and was recently (accidentally or deliberately) introduced far from its

54 natural distribution area to many places in the world, such as Israel, Hawaii, Florida, the Greater

55 Antilles, and the Lesser Antilles, probably including Guadeloupe (Breuil, 2013; Falcón et al.,

56 2013; Henderson and Breuil, 2012; Krauss et al., 2014; Pasachnick et al., 2012). Endemic

57 populations also seem to occur on some of the Lesser Antillean islands, such as Saba, Montserrat,

58 and Saint Lucia (Breuil, 2013; Malone and Davis, 2004; Morton, 2009; Stephen et al., 2013).

59 Conversely, *I. delicatissima* is endemic to the Lesser Antilles. It is now considered to be an

60 endangered species on the most recent IUCN red list (Breuil et al., 2010), as it is now extinct on

61 most of the islands in Guadeloupe (Breuil, 2002; Henderson and Breuil, 2012), and is currently

62 the focus of an international plan of action (Knapp et al., 2014). Recent genetic data show little

63 divergence between the different Lesser Antillean populations and suggest that this animal may

64 have spread to the islands recently, possibly as a result of human activity (Martin et al., 2015;

65 Vuillaume et al., 2015). This hypothesis is congruent with the paleontological results obtained

66 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

90   prehistorically (Martin, 2009; Martin et al., 2010); a finding that contradicts the notion that *I.*

91   *iguana* would be a recently introduced species. An early occurrence of *I. iguana* was also

92   advanced by Lazell (1973), who stated that "no human introduction is responsible for the

93   presence of *Iguana iguana* anywhere in the Lesser Antilles". However, the conclusions proposed

94   by Martin (2009) and Martin et al. (2010) based on archaeological specimens are questionable,

95   since a recent study conducted by Bochaton et al. (2016b), focusing on the osteological

96   differences between the two *Iguana* species, has shown that most of the osteological

97   characteristics used up until now are unreliable. Consequently, a review of the archaeological

98   material using new reliable identification criteria was necessary in order to analyze variations in

99   the taxonomic composition of *Iguana* in archaeological assemblages from the Guadeloupe

100 Islands throughout time. In addition, the reconstruction of the past snout-vent length (SVL) of

101 archaeological *Iguana* (Bochaton, 2016) allows for size comparisons with modern populations.

102 The aim of this paper is to provide a new analysis of osteological *Iguana* remains from 25

103 Guadeloupian archaeological sites using new methodological tools developed for the

104 identification (Bochaton et al., 2016b) and zooarchaeological study (Bochaton, 2016) of

105 archaeological *Iguana* remains. These newly obtained zooarchaeological data are then compared

106 with data collected from modern *Iguana* on the Guadeloupe Islands, as well as textual historical

107 data. Finally we use the results to provide evidence of the occurrence of *Iguana* species and

108 morphological changes through time, and describe interactions between past humans and iguanas

109 on the Guadeloupe Islands.

110 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

134 (Mesoindian or Archaic Age), but indirect evidence of human occupation in the form of increased

135 charcoal particles, presumably from human-induced fires, suggests that settlement could have

136 been earlier, ca. 3000 cal. BC. (Siegel et al., 2015; Stouvenot et al., 2014). Morel I on Grande-

137 Terre is the oldest ceramic archaeological site in Guadeloupe Islands dating to around AD 80 and

138 attributed to the Huecan Saladoid culture (Neo-Indian or Early Ceramic Age) (Bérard, 2013;

139 Clerc, 1964; Fitzpatrick, 2015; Hofman et al., 1999; Romon et al., 2006).

140 This early Saladoid component includes Cedrosan Saladoid ceramic traditions, which occurred

141 between AD 300-900 and evolved into the Marmoran Troumassoid tradition that lasted from AD

142 900-1500 (i.e., the Late Ceramic Age) (Bonnissent, 2008; Honoré, 2014; Keegan et al., 2013).

143 After Columbus' second trip in 1493 and a period of contact between Amerindian and European

144 populations archaeologically characterized by Cayo complex ceramics, French colonization

145 began around 1635 and led to the disappearance of Amerindian populations (Keegan et al., 2013;

146 Saunders, 2005).

147 3. Material and Methods

148 3.1 Zooarchaeological material

149 The osteological material included in this study comes from 25 pre-Columbian archaeological

150 sites situated on Grande-Terre (5), Basse Terre (7), Les Saintes (1), Îlets de Petite Terre (4), La

151 Désirade (3) and Marie-Galante (5) (Fig. 1; Supplementary material S1; Tab. 1). The

152 chronological or cultural attribution of these sites is reported in Supplementary material S1 and

153 Tab. 1. Most of the sites with the *Iguana* remains studied here had already been investigated by

154 zooarchaeologists who studied the whole bone assemblages recovered in these archaeological

155 deposits (de Waal, 2006; Grouard, 2010, 2007, 2001). For this study, the complete assemblage of

156   skeletal remains collected from each site was observed in order to review previously identified

157   *Iguana* remains and, when possible, to add newly identified remains. In total, 2,236

158   archaeological *Iguana* remains were collected from the different assemblages and investigated as

159   part of this study.

160   3.2 Methodology

161   Specific identifications followed the osteological characters described by Bochaton et al. (2016b).

162   The latter study is based on a large sample of modern *Iguana* (69 skeletons) and proposes a series

163   of 32 identification criteria distributed among 17 different skeletal (both cranial and postcranial)

164   elements allowing for the distinction of *I. delicatissima*, *I. iguana*, and for some characters,

165   hybrids of the two species. The authors also provided a percentage of reliability for each criterion

166   in order to allow for the discussion of the results. In the present study, archaeological bones that

167   did not present discriminating characters according to Bochaton et al. (2016b) were left

168   specifically unidentified as *Iguana* sp.

169   The Snout-Vent Length (SVL) estimations of archaeological specimens were obtained using the

170   measurements and predictive equations described by Bochaton (2016) on the different anatomical

171   elements. Skeletal maturity was estimated on the basis of the fully or partially ossified status of

172   each bone and the maturity stages also described by Bochaton (2016). Skeletal maturity and size

173   data were then combined to obtain a "Minimal Theoretical Maximal Size" or MTMS, used to

174   estimate the size that the archaeological specimen would have reached if it had lived until the end

175   of its growth. This MTMS is estimated by considering that the largest immature long bone

176   provides an SVL estimation of a maximum of 80% of the maximal size of the specimen

177   (Bochaton, 2016; Maisano, 2002). Data concerning the size of the modern Guadeloupian *I.*

178 *delicatissima* were collected by the French Office National de la Chasse et de la Faune Sauvage

179 (ONCFS) on La Désirade in 2012 (funded by the French state and FEDER) and by the NGO Le

180 Gaiac association on Îlets de Petite Terre (Terre-de-Haut and Terre-de-Bas) between 2007 and

181 2011, and were made available to us for study.

182 The minimum number of individuals (MNI) was calculated using the most abundant anatomical

183 element for each site (Shipman, 1981). The global MNI is an addition of the MNI obtained from

184 the different sites considering that it is highly unlikely that a specimen would be divided among

185 different deposits. To study the anatomical distribution of bone remains we used the

186 "Proportional Representation of each skeletal part" (PR) (Dodson and Wexlar, 1979).

187 Statistical analyses were performed using the free software "R" (version 3.1, https://cran.r-

188 project.org/) and "R Studio" (version 0.98.1102). Data normality was tested using the Shapiro-

189 Wilk test. As data were not normally distributed, comparisons between two populations were

190 performed using the Wilcoxon test and comparisons between more than two populations using

191 the Kruskal-Wallis test. Differences were considered to be statistically significant for P value

192 <0.01.

193 Finally, in order to observe traces hypothetically left by humans on *Iguana* bones, all the remains

194 were carefully observed using a stereomicroscope (Nikon SMZ1000). In addition, Scanning

195 Electron Microscope (SEM) photographs of digested bones were taken.

196

197 4. Results

198 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 basipterygoid 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

223   the articular bone, the length of the retroarticular process is inferior to 150% of the length of the

224   articular fossa and the tympanic crest is wider than the angular crest; On the surangular bone

225   (Fig. 2), the surangular coronoid process is pointed; On the axis vertebra, the ratio between the

226   minimal neural arch length and the posterior neural arch breadth comprising the

227   postzygapophysis is inferior to 0.65; All the caudal vertebrae lack caudal autotomy planes; On

228   the scapulocoracoid bone, the small posterolateral protuberance marking the attachment of the

229   scapulohumeral ligament is absent; On the pelvic bone, the ilium dorsal crest is convex and bears

230   a short and curved ventral edge, the posterior section of the ilium is subtriangular, the anterior

231   section of the pubis forms a triangle with an acute apex angle, and the posterior margin of

232   ischium is more concave than in *I. iguana*; On the humerus (Fig. 2), the foramen of the

233   supracondylar fossa is more open than in *I. iguana*.

234   However, three remains (0.1%) presented the following *Iguana iguana* characteristics: an

235   infraorbital foramen posteriorly located on a maxilla, and an exonarinal margin of the facial

236   process forming a right angle with the premaxillary process in lateral view on the same bone; an

237   intramandibular lamella anteriorly extended under the four last dental positions on a dentary, and

238   a narrow foramen of the supracondylar fossa on a humerus.

239   4.2 Body size characteristics of *Iguana* archaeological populations

240   Past Snout-Vent Length (SVL) and skeletal maturity were observed on all the studied *Iguana*

241   remains. Past Snout-Vent Length (SVL) estimations were obtained from 488 *Iguana* remains

242   (MNI=48) from all skeletal parts for which size predictive equations were defined by Bochaton

243   (2016). These remains come from all of the archaeological sites included in this study and a list

244   of all the obtained estimations can be found in Supplementary material (S2).

245　The estimated size ranged from around 70 mm SVL for small newborn specimens to very large

246　individuals with SVL of more than 500 mm (Fig. 3, Supplementary material S2). However, all

247　size classes were not equally distributed in our assemblage. Specimens smaller than 220 mm SVL

248　were nearly absent and most fossil *Iguana* had a SVL between 300 and 400 mm. Specimens

249　smaller than 220 mm SVL (between 70 and 150 mm SVL) only occur in Morne-Rita on Marie-

250　Galante Island (NMI=1), Cathédrale de Basse-Terre on Basse Terre Island (NMI=1) and Anse à

251　la Gourde on Grande-Terre Island (NMI=2) (Fig. 3, Supplementary material S2).

252　Skeletal maturity data (bone ossification) were recorded on 223 archaeological *Iguana* remains.

253　Among them, 65 (29%) were mature bones of which 35 belong to fully-grown specimens (with

254　fully ossified long bones and/or fused sacral vertebrae = stage 4 *sensu* Bochaton, 2016). The

255　other 158 remains (71%) correspond to non-fully grown individuals and at least 13 of them

256　belong to non-sexually mature specimens (for which the pelvic girdle and axis are not fully

257　ossified = stage 2 *sensu* Bochaton, 2016).

258　Moreover, 114 remains yield a combination of both size and skeletal maturity data and thus allow

259　for the estimation of the MTMS and the size range of the previously defined maturity stages. The

260　detailed observation of archaeological *Iguana* sizes was performed at the island scale because the

261　material was too scant to obtain significant results for each site. In addition, we noted that

262　archaeological specimens collected from the different Guadeloupe islands present SVL

263　differences (Kruskal-Wallis test, p.val<0.01) (Fig. 3). Size overlap often occurred between the

264　defined maturity stages. This could reflect a size estimation error linked to measurement error,

265　variability in bone maturation timing or could also be the result of sexual size dimorphism.

266 On Marie-Galante, the Minimal Theoretical Maximal Size (MTMS) of archaeological *Iguana*

267 was 475 mm, and the estimated SVL mean was 324 mm (Fig. 3-A). A size overlap of a maximum

268 of 40 mm was observed between the maturity stages. The results were similar for the sites from

269 Îlets de Petite Terre (Fig. 3-B), La Désirade (Fig. 3-C), and Grande-Terre (Fig. 3-D): MTMS are

270 respectively 462, 460 and 475 mm with mean estimated SVL of 330, 358 and 310 mm

271 respectively. On Îlets de Petite Terre and Grande-Terre, some limited size overlap (between 19

272 and 25 mm) was observed between maturity stages. A single archaeological SVL datum (361

273 mm) was collected from Les Saintes Island.

274 The situation was more complex for archaeological *Iguana* from Basse Terre Island, as two

275 groups of very different sizes seem to occur in the same archaeological contexts. Most of the

276 specimens are larger than any other observed specimens, with estimated sizes between 400-450

277 mm SVL for non-fully mature bones (MNI=1), reaching a maximum of 511 mm SVL for fully

278 mature bones (MNI=2) (Fig 3-E). However, some specimens (MNI=2) present estimated sizes of

279 only 323 and 388 mm SVL for fully mature bones. This situation led to an important body size

280 overlap between maturity stages and made the definition of a single MTMS impossible.

281 Consequently, we defined two MTMS on the basis of the smallest mature and largest immature

282 bones and obtained MTMS of respectively 403 mm and 556 mm SVL (Fig. 3-E). These two

283 MTMS correspond to two populations presenting different body sizes. Taken as a whole, the

284 estimated SVL of Basse Terre archaeological iguanas (mean= 364 mm) were the highest for the

285 archipelago.

286 We did not observe any effects of chronological attribution (Saladoid or Troumassoid) on the size

287 of the *Iguana* remains (Wilcoxon test, p.val=0.34). However, comparisons of SVL data collected

288 from modern *I. delicatissima* populations from La Désirade (n= 274) and Îlets de Petite Terre

289   (Terre-de-Haut and Terre-de-Bas) (n=435) with all archaeological SVL data obtained from these

290   islands show that archaeological iguanas were far larger than modern specimens (Wilcoxon test,

291   p.val <0.001). Indeed, modern iguanas from three islands do not exceed 390 mm SVL (max. 390

292   mm on Terre-de-Haut [see also Breuil, 2002], 385 mm on Terre-de-Bas and 360 mm on La

293   Désirade [387 mm following Schardt, 1998), whereas archaeological iguanas from the same

294   islands can be larger than 450 mm SVL. The SVL mean of archaeological iguanas (330-358 mm)

295   was also higher than the SVL mean of modern iguanas (258-274 mm), but as the specimens

296   occurring in archaeological sites and measured in the field are probably subject to very different

297   sampling methods, SVL means are nearly impossible to interpret. A very dry season in 2001 led

298   to high mortality among iguanas from La Désirade and Petite-Terre islands (Breuil, 2002) and

299   could have contributed to the elimination of large specimens. However, archaeological iguanas

300   from these islands are still larger than any modern *I. delicatissima* ever measured in the Lesser

301   Antilles, and a reduction in size during the modern period is very likely.

302   4.3 Skeletal distribution, anthropic marks, and surface alterations of the archaeological remains

303   Due to the scarcity of *Iguana* remains in archaeological sites, we did not find clear site-scale

304   differences in the data presented in this section. Consequently, all the sites were treated as a

305   whole, but unusual observations encountered at single sites are also mentioned when pertinent.

306   The overall representation of skeletal parts was low (PR=12.5%), which means that on average

307   only 12% of *Iguana* skeletons were present in the archaeological sites, but all the anatomical

308   parts were represented. The most represented anatomical parts are the proximal part of the tail

309   (PR=42), femur (PR=32), humerus (PR= 29), middle part of the tail (PR=28), pelvic girdle

310   (PR=25), dorsal vertebrae (PR=24), and tibia (PR=22) (Fig. 4). These anatomical parts are the

14

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

334   (Fig. 6-A), and the destruction of most of their teeth. Such traces were probably left by humans,

335   carnivores, or diurnal raptors (Andrews, 1990; Stoetzel et al., 2012).

336   5. Discussion

337   5.1 Taxonomic identification of archaeological iguanas

338   Among the 410 archaeological remains identified to the species level, 407 were attributed to *I.*

339   *delicatissima* and only three to *I. iguana*. However, these *I. iguana* identifications are highly

340   uncertain. Indeed, two of them (a maxilla and a humerus from the Basse-Terre Gare Maritime

341   site) were identified using characteristics that are not considered to be 100% reliable (Bochaton et

342   al., (2016b). They could represent misidentifications in view of the large number of studied

343   archaeological remains. The third bone presenting an *Iguana iguana* characteristic is a dentary

344   from the Tourlourous site on Marie-Galante. It was identified based on a 100% reliable character

345   (character I from Bochaton et al., 2016b). However, this attribution is still dubious as the bone is

346   very isolated in an assemblage where 99.7% of the remains were unambiguously attributed to *I.*

347   *delicatissima*. Given this context, a single remain bearing an *I. iguana* character is clearly

348   insufficient to consider the occurrence of that species at the Tourlourous site. The most likely

349   explanation is that the diagnostic characteristic described for the dentary by Bochaton et al.,

350   2016b is not 100% reliable. This would not be surprising considering the important skeletal

351   morphological overlap between *I. iguana* and *I. delicatissima* described by previous authors and

352   the limited number of available comparative specimens. Consequently, *I. delicatissima* seems to

353   be the only *Iguana* species occurring on the Guadeloupe Islands during pre-Columbian times and

354   there is no clear evidence of the occurrence of *I. iguana* during that period. In addition, the

355   extreme scarcity of *I. iguana* elements in our material shows that these *I. delicatissima*

16

356 populations bear no traces of past hybridization with *I. iguana*. These results differ from those

357 obtained by Martin (2009) and Martin et al. (2010), who stated that both *I. iguana* and *I.*

358 *delicatissima* occurred prehistorically on the Guadeloupe Islands. This contradiction is

359 undoubtedly due to the unreliability of the identification characters used by these authors

360 (Bochaton et al., 2016b).

361 Consequently, previous results should no longer be taken into account and we should currently

362 consider that there is no evidence of past occurrences of *I. iguana* on the Guadeloupe Islands

363 prior to European contact. This conclusion can be related to the long-standing discussion

364 concerning the introduced or native status of *I. iguana* in the Lesser Antilles. The introduced

365 status of *I. iguana* was first suggested by Dunn (1934) and then Underwood (1962), but

366 subsequently refuted by Lazell (1973). Later, Lescure (1983) suggested an Amerindian role in the

367 dispersal of *I. iguana* in the Antilles and more recently Breuil (2013, 2002), Breuil et al. (2010)

368 and Vuillaume et al. (2015) assumed that *I. iguana* was introduced to the Guadeloupe Islands and

369 St Maarten during the 19th and 20th centuries. Our results concur with the latter hypothesis and

370 should contribute to addressing this long-standing debate.

371 5.2 Size of past iguanas

372 Moreover, we investigated the past size of *I. delicatissima* in the Guadeloupe Islands for the first

373 time. In order to achieve this, we observed two estimated size variables; the mean SVL and

374 Minimal Theoretical Maximal Size (MTMS) of past iguanas from each island and found that

375 these variables showed conflicting results. Indeed, although both variables showed inter-island

376 differences, the mean SVL indicated that past iguanas were larger on Basse Terre and La

377 Désirade than on Marie-Galante and Îlets de Petite Terre (Terre-de-Bas), and even smaller on

378 Grande-Terre (Fig.3). Conversely, the MTMS (between 460 and 475 mm SVL) indicated that

379 iguanas were of similar size on all the islands with the exception of Basse Terre, where they were

380 larger (Fig.3). The advantage of the MTMS value is that it also takes account of the skeletal

381 maturity of past iguanas and not simply their size. Thus, it allows for the study of the body size of

382 archaeological populations of consumed animals, with often strongly biased size composition: we

383 clearly demonstrated a size selection by human hunters on the studied archaeological iguanas (see

384 below). Thus we consider the mean body size differences observed on archaeological iguanas

385 from the different islands as a bias induced by differential sampling selection by past humans

386 rather than true biological differences.

387 Consequently, we assume that the past size of *I. delicatissima* was similar on Marie-Galante, Îlets

388 de Petite Terre (Terre-de-bas), La Désirade and Grande-Terre. However, larger iguanas occurred

389 on Basse Terre Island, as shown by the MTMS (superior to 550 mm). The larger sizes observed

390 on that island could be linked to indirect geographic and environmental effects. On account of its

391 volcanic nature, Basse Terre is more humid and presents more mountainous zones and habitat

392 diversity than the limestone islands (Lasserre, 1961; Lescure, 1987). It is also noteworthy that the

393 biggest modern *I. delicatissima* ever measured on Guadeloupe Islands (410 mm SVL) originated

394 from that island (Breuil, 2002). However, smaller archaeological specimens (MTMS= 403 mm)

395 were also recovered from Basse Terre. Size differences between these small and large iguanas

396 occurring on Basse Terre are far too high to be related to the same sexual dimorphism as in

397 modern *I. delicatissima,* which does not appear to be as marked according to the ONCFS data

398 collected on La Désirade and Petite Terre (a difference of 20 mm in SVL between the largest

399 measured female and male) and to data collected on Dominica (a difference of 42 mm in SVL

400 between the largest measured female and male) (Knapp et al., 2016), or to a size estimation error.

401   It is possible that sexual dimorphism may have been more marked in Basse Terre iguanas than in

402   modern iguanas but genetic or isotopic data would be needed to confirm this hypothesis. Another

403   alternative explanation is that these small iguanas could correspond either to an isolated local

404   population subject to unfavorable biotic and/or abiotic conditions or exogenous iguanas

405   translocated by pre-Columbians from another island.

406   5.3 Pre-Columbian population interactions with iguanas

407   The similarity in size of *I. delicatissima* indicated by the MTMS on most islands, including

408   Marie-Galante (Fig. 3), where they were probably introduced (Bochaton et al., 2015), could also

409   point to their introduction to other islands (see also Vuillaume et al., 2015), possibly by human

410   populations, probably for feeding purposes. However, this hypothesis lacks theoretical grounds

411   considering that island size only has a slight effect on squamate body size (Meiri, 2007) and this

412   similarity in size could also be the consequence of convergent evolution. The occurrence of

413   *Iguana delicatissima* remains in most of the Guadeloupian pre-Columbian archaeological sites

414   indicates that these large lizards were collected by human pre-Columbian populations for two

415   thousand years (from 500 BC to AD 1500), possibly using specific hunting strategies. Indeed,

416   hunted iguanas were not randomly selected, as suggested by archaeological *Iguana* size

417   distribution, which does not reflect natural population size ranges. Most of the archaeological

418   assemblages exclusively include large iguanas (mainly between 300 and 400 mm SVL) and

419   young individuals (with SVL of less than 180 mm) are largely absent from archaeological

420   deposits (Fig. 3). Although archaeological collection methods (for instance, the use of sieves and

421   mesh size) could influence the observed size distribution, they cannot account for the lack of

422   medium-sized individuals, as smaller taxa occur at all of the investigated sites. Thus, the

423   observed distribution is likely to reflect human selection of the largest animals, which provide the

424 most meat, and points to the difficulties involved in catching young iguanas or to the lack of

425 interest they present in terms of meat intake. However, this size selection seems to differ between

426 islands. Indeed, the difference between the MTMS of iguanas from each island and the average

427 size observed in the archaeological sites of the same island differs among islands. These

428 differences can be interpreted in terms of selection intensity: lower differences between the mean

429 size and the MTMS point to the more marked selection of large specimens. This difference is

430 especially low on La Désirade and Îlets de Petite Terre (102-132 mm), where selection seems to

431 be strongest. However, it is higher in Marie-Galante and Grande-Terre (151-165 mm), and even

432 higher in Basse Terre (192 mm), where selection appears to be low. The strong selection of large

433 specimens on La Désirade and Îlets de Petite Terre could reflect the high density of *Iguana*

434 populations, and thus the wide choice available to hunters, whereas conversely, population

435 density would have been lower on Marie-Galante and Grande-Terre. The results from Basse

436 Terre, indicating populations of different body-size, were difficult to assess. In the light of these

437 data it is interesting to observe that Îlets de Petite Terre and La Désirade are the only islands in

438 Guadeloupe still inhabited by large populations of *I. delicatissima* (Breuil, 2002). This could

439 perhaps be explained by their isolation and high population density, preserving them from

440 extirpation.

441 This clear size selection applied to archaeological specimens reflects the hunter's capacity to

442 select hunted specimens and thus indicates the use of specific hunting techniques. No evidence of

443 injuries was observed on these bones, but historical sources from European authors describing

444 mid-17th century Amerindians provide useful information about how pre-Columbian iguanas may

445 have been hunted. These authors indicated that iguanas were caught by Carib Indians using a

446 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

470   predators. Thus, for the digested remains found at the open-air archaeological sites in Anse à la

471   Gourde, one of the most plausible hypotheses would be that these small iguanas were hunted by

472   domestic dogs, since dogs occur in archaeological sites and were part of the daily life of pre-

473   Columbian populations in the Guadeloupe Islands (Grouard, 2001; Grouard et al., 2013).

474   Alternatively, some of the remains collected in cave deposits (Anse à l'Ecu, Morne-Rita and

475   Cadet 3) may reflect predation by birds of prey.

476   5.4 Size evolution of *Iguana delicatissima* over time

477   Several hundreds of years of pre-Columbian hunting do not seem to have impacted *I.*

478   *delicatissima* populations, in contrast to the activities of modern human populations. Indeed,

479   according to archaeological evidence, the size of iguanas seems to remain stable throughout the

480   pre-Columbian period. Conversely, comparisons with modern data collected on Îlets de Petite

481   Terre (Terre-de-Haut and Terre-de-Bas) and La Désirade, the only two islands in Guadeloupe

482   still densely inhabited by *I. delicatissima*, show a possible significant decrease in size between

483   pre-Columbian and modern times, estimated at about 20% of *I. delicatissima* SVL size. In

484   addition, no present-day *I. delicatissima* equivalent in size to the largest archaeological iguanas

485   has ever been measured, since the highest SVL ever recorded on a *I. delicatissima* specimen is

486   only 430 mm SVL (from Dominica; Day et al., 2000), as opposed to a maximum of 550 mm SVL

487   for the largest archaeological specimen. As a precaution we should nevertheless note that it is

488   difficult to assess the reliability of extreme archaeological SVL values, especially for the largest

489   archaeological specimens with a SVL of more than 500 mm. This is because such sizes exceed

490   the size of the modern specimens used by Bochaton (2016) to construct SVL estimation

491   equations. However, such very high sizes are close to the size of the iguanas described by Du

492   Tertre in Guadeloupe during the 17th century, when a total length of 160 cm corresponds to an

493   SVL of around 53 cm (Du Tertre, 1667).

494   However, although no equivalent sized *I. delicatissima* has ever been measured or collected, this

495   does not mean that it never existed. Indeed, Lazell (1973) mentioned that the small size of *I.*

496   *delicatissima* in museum specimens could be due to sampling bias. He also claimed that he saw

497   large specimens in Les Saintes and Dominica, with an SVL of around 400-450 mm, an

498   observation confirmed on Dominica where the largest modern iguanas attain a maximal SVL size

499   of 428 mm (Knapp et al., 2016). Still, even if the accuracy of estimated past iguana size is

500   difficult to assess, a significant decrease in the size of this lizard on the Guadeloupe Islands over

501   the past few centuries seems likely. As a consequence, the decrease in squamate size during the

502   Holocene previously highlighted by Pregill (1986) in other West-Indian squamates also seems to

503   apply to *I. delicatissima* from the Guadeloupe Islands. This constitutes further evidence of the

504   strong impact of human populations after the European colonization of these islands, where *I.*

505   *delicatissima* populations were well established and healthy, as suggested by their large size,

506   despite extensive exploitation by pre-Columbian hunters. These results differ from those obtained

507   by Carlson and Keegan (2004) on Grand Turk Island (Greater Antilles), where pre-Columbian

508   hunting seemed to result in a size diminution in rock iguanas, probably on account of over-

509   exploitation on a relatively small island (only 18 km²). But this phenomenon concerns pre-

510   ceramic populations relying largely on terrestrial fauna for food sources (40% of the MNI of the

511   Grand Turk Island site corresponds to iguanas). Conversely, the archaeological sites concerned

512   by our study concern more recent ceramic cultures that rely mainly on marine resources and

513   squamate remains represent a very minor part of the osteological assemblages (below 6% and

514   often less than 1% of the vertebrate remains collected in each site [de Waal, 2006; Grouard, 2010,

515 2007, 2001; Bochaton, work in progress]). Up until now, few data were available concerning the

516 pre-ceramic cultures and their subsistence strategies on the Guadeloupe Islands, and iguanas from

517 these periods, as well as from pre-anthropic periods, remain unknown to us.

518 6. Conclusion

519 Our data clearly show that populations of *Iguana delicatissima*, were formerly present on all of

520 the Guadeloupe Islands during pre-Columbian times and that at the same period, the invasive

521 species, *I. iguana* was absent, confirming that it was introduced to this archipelago during the

522 past few centuries. Iguanas were the object of selection focusing on large specimens by pre-

523 Columbian hunters, as attested by the size reconstruction of archaeological specimens. The meat

524 from these lizards was cooked and consumed by Amerindians, as described in historical sources

525 recounting the daily life of 17th century Caribbean Amerindians. Hunting by pre-Columbian

526 hunters had no visible effect on past iguana populations. However, comparisons with modern

527 data demonstrate that *I. delicatissima* is now extinct on most of the Guadeloupe Islands and is

528 20% smaller on the islands where it still occurs. This fact highlights the massive impact of

529 European and historical populations on these large lizards, which mostly became extinct or

530 underwent a drastic decrease in body size over the past three centuries. Such phenomena

531 impacting iguanas were also observed using archaeological or subfossil data for several other

532 taxa in the Caribbean (MacPhee, 2009; Steadman et al., 2015; Stoetzel et al., 2016) and in other

533 geographic areas (Grayson, 2001; Nakamura et al., 2013; Steadman, 1995). They provide further

534 evidence of the strong impact of modern societies on fauna in the context of the current

535 biodiversity crisis (Barnosky et al., 2011; Burney and Flannery, 2005; Ceballos et al., 2015).

536 Similar studies to ours would allow for the observation of past hitherto hidden or inaccurately

537 recorded phenomena, such as the timing of colonization, spatio-temporal morphological changes

538 throughout time or the natural or human-mediated introduction of exogenous species. They

539 would also lead to the testing of several hypotheses based on modern data. However, with regard

540 to archaeological lizards and snakes, such studies are extremely rare (de Buffrénil and Hemery,

541 2007; Klemens and Thorbjarnarson, 1995; Monchot et al., 2014) and much work remains to be

542 done in order to elucidate recent squamate history and interactions of these animals with past

543 human populations all over the world.

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| Island	Site	Date	*Iguana delicatissim*	*Iguana iguana*	*Iguana* 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**

782   Table 1: Number of *Iguana* remains (NR) collected from each archaeological site along with their

783   attribution to *I. delicatissima*, *I. iguana* or *Iguana* sp. and Minimal Number of Individuals (MNI).

784   Cultural attribution of each deposit is also indicated: Archaic= 2000 - 500 BC, Saladoid = AD 80

785   - 900, Troumassoid = AD 900 - 1490, Modern=1493 – present.
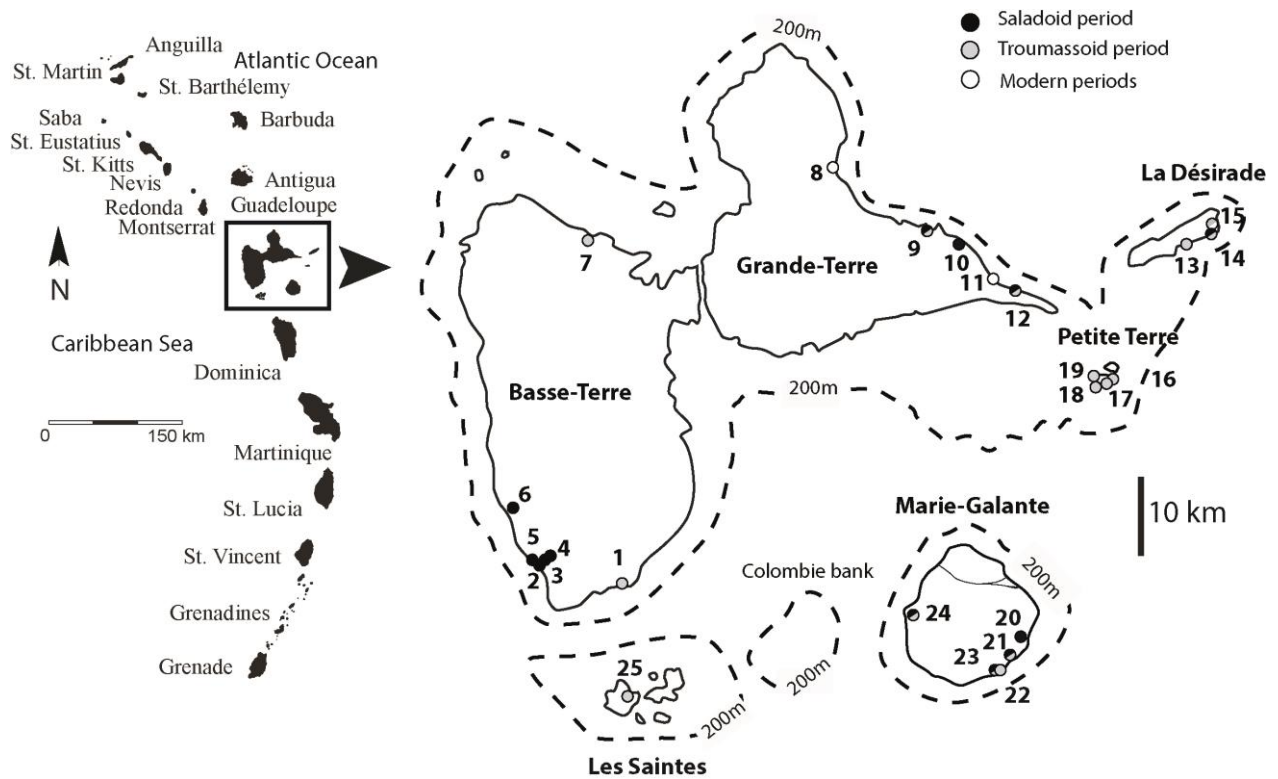
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787   Figure 1: Map of the Lesser Antilles and focus on the Guadeloupe Islands with isobaths (-200m)

788   from Münch et al. (2013) and location of the studied archaeological sites with their chronological

789   attributions (Saladoïd period (AD 80 - 900), Troumassoid period (AD 900 - 1500) or Modern

790   period (AD 1493 – present): 1: Grande-Anse Trois Rivières; 2: 24, rue Schoelcher; 3: Place

791   Saint-François; 4: Cathédrale de Basse-Terre; 5: Gare Maritime de Basse-Terre; 6: Embouchure

792   de la Rivière Baillif; 7: Sainte-Rose La Ramée; 8: Grotte de l'Anse à l'Ecu; 9: Morel; 10: Anse à

793   l'Eau; 11: Grotte de l'Anse à la Gourde; 12: Anse à la Gourde; 13: A l'Escalier; 14: Petite Rivière;

794   15: Pointe Gros Rempart 6; 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.
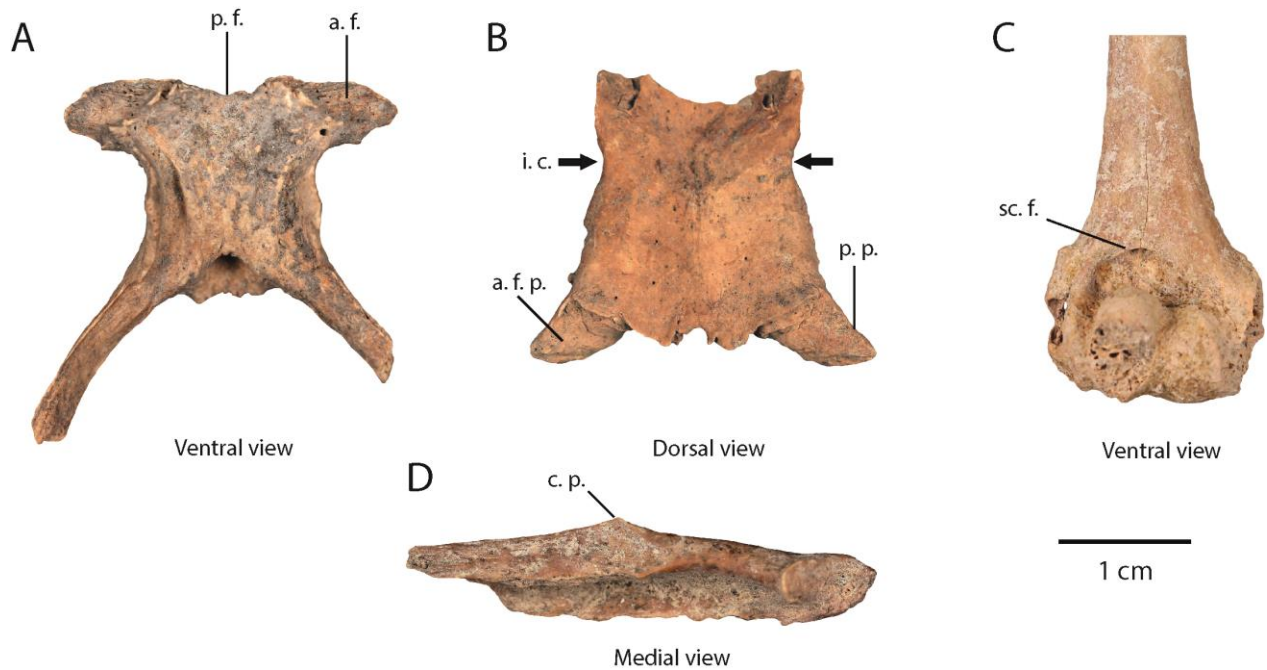
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798 Figure 2: Examples of *Iguana* bone remains from the Gare Maritime site (Basse Terre),

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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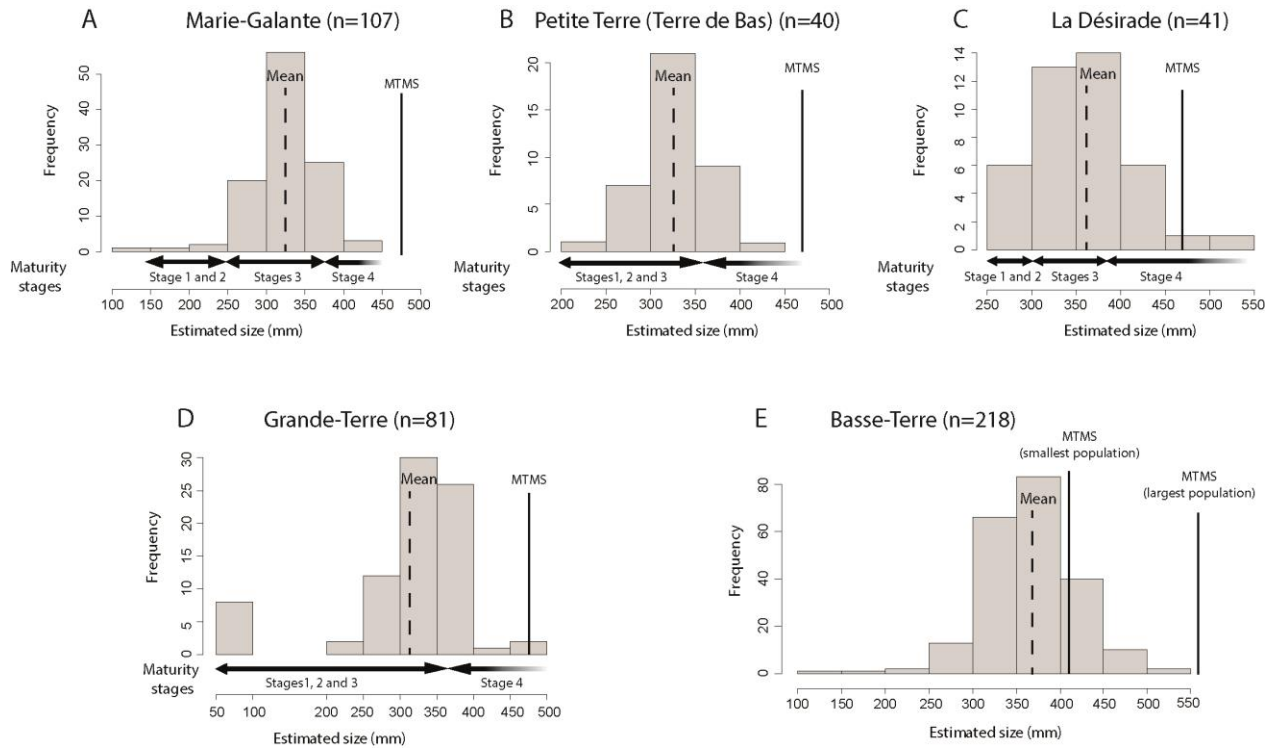
Figure 3: Distribution of estimated SVL size (in millimeters) obtained on archaeological *Iguana* remains from A: Marie-Galante, B: Îlets de Petite Terre, C: La Désirade, D: Grande-Terre and E: Basse Terre islands. The Minimal Theoretical Maximal Size (MTMS) is provided for each island along with the correspondence between size and skeletal maturity stages defined by Bochaton (2016).
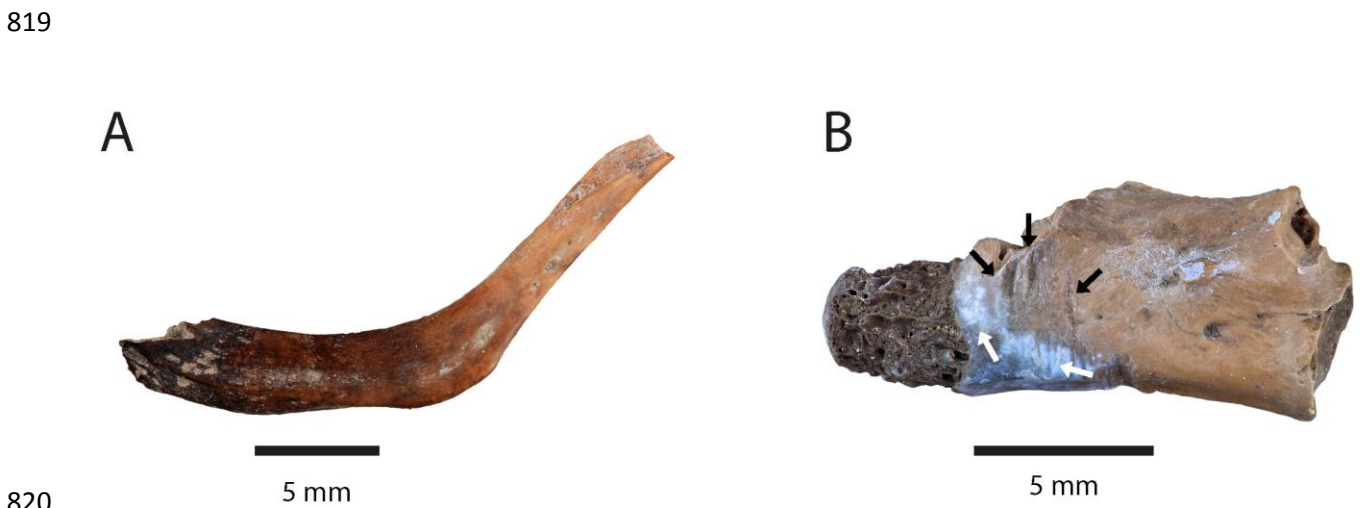
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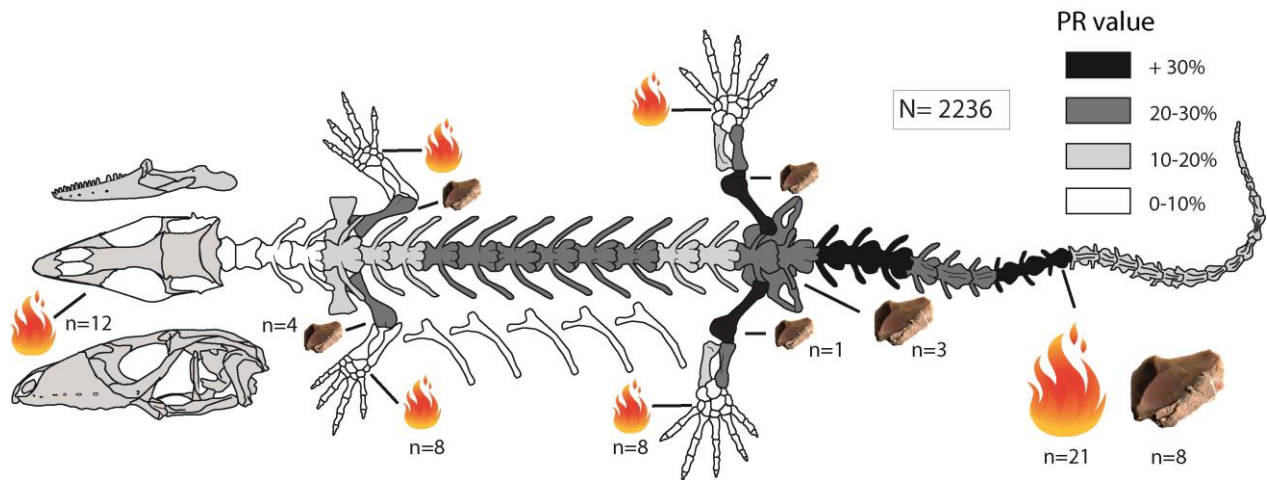
Figure 4: Anatomical distribution of *Iguana* remains from the 25 sites with PR value (Dodson and Wexlar 1989) for each anatomical part along with the occurrence of fire traces (fire symbol) and cut marks (modern flint tool symbol) on the extremities of the skeleton (skeleton drawing modified from Coutureau, 2004).
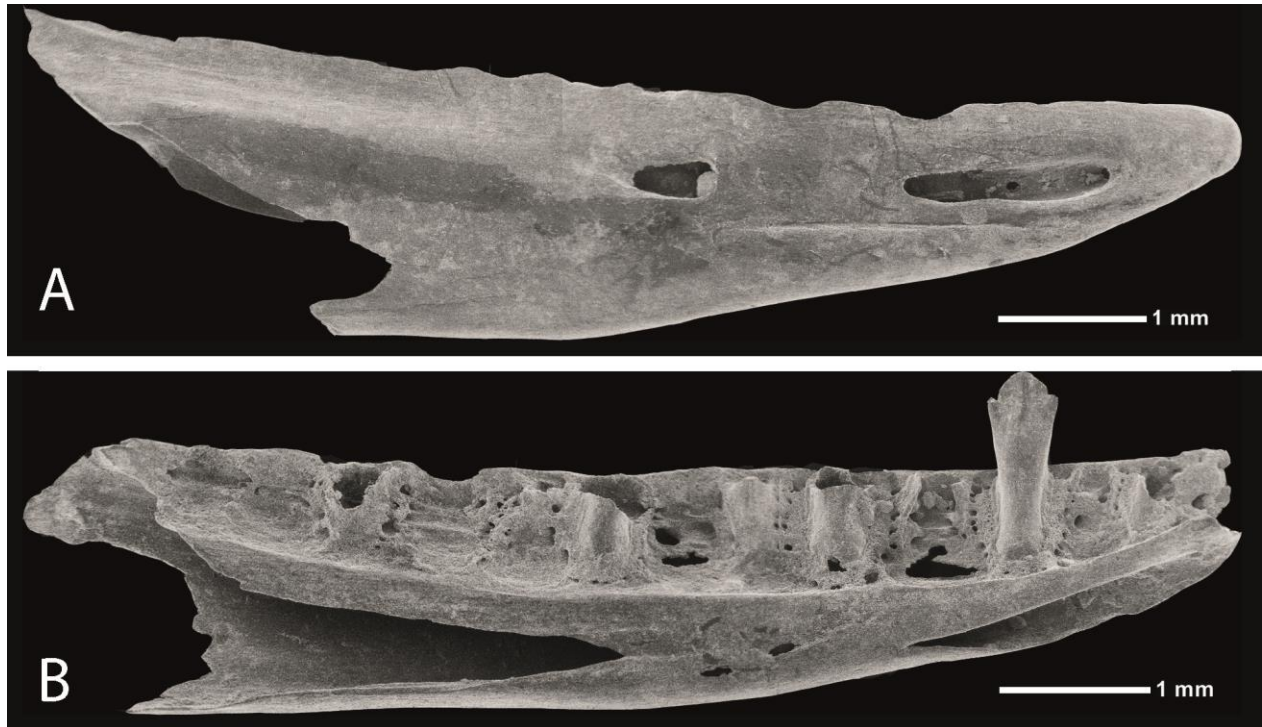
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Figure 5: A) Half-burnt (black) left jugal bone of *I. delicatissima* from Caille à Bélasse site (Square O51c – dec11). B) Caudal vertebra of *I. delicatissima* in lateral view with white burning

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.