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1 **Historical and fossil evidence of an extinct endemic species of *Leiocephalus***  
2 **(Squamata: Leiocephalidae) from the Guadeloupe Islands**

3 CORENTIN BOCHATON<sup>1,2</sup>, LAURENT CHARLES<sup>3</sup> & ARNAUD LENOBLE<sup>1</sup>

4 1- PACEA – UMR CNRS 5199, Université de Bordeaux, 33 615 Pessac, France. [corentin.bochaton@u-](mailto:corentin.bochaton@u-bordeaux.fr)  
5 [bordeaux.fr](mailto:corentin.bochaton@u-bordeaux.fr); [arnaud.lenoble@u-bordeaux.fr](mailto:arnaud.lenoble@u-bordeaux.fr)

6  
7 2 - Max Planck Institute for the Science of Human History, Department of Archaeology, Kahlaische Straße 10,  
8 07745 Jena, Germany.

9 3- Muséum de Bordeaux - sciences et nature, 5 Place Bardineau, Bordeaux 33 000, France. [l.charles@mairie-](mailto:l.charles@mairie-bordeaux.fr)  
10 [bordeaux.fr](mailto:l.charles@mairie-bordeaux.fr)

11 **Abstract**

12 Documenting recent extinction events against the backdrop of increasing human-induced  
13 environmental pressure is complicated by the lack of historical and subfossil evidence for most parts  
14 of the world. This paucity of data renders it particularly difficult to evaluate the human impact on  
15 fragile environments, such as small islands, that may have been heavily altered by historical human  
16 exploitation. Here we describe a new species of an extinct *Leiocephalus* lizard from Guadeloupe,  
17 *Leiocephalus roquetus* sp. nov. based on recent discoveries of both a previously undocumented  
18 historically taxidermy specimen and of a large assemblage of subfossil bone remains from La Désirade  
19 Island. This new species presents a primitive morphology compared to all extant species of its genus  
20 and provides evidence for the past existence of a Lesser Antillean clade of *Leiocephalus* lizards that  
21 was completely wiped out in the centuries following the European colonization of these islands. Our  
22 study demonstrates how paleontological approaches can help to better understand the history of human  
23 environmental impact as well as the degree of degradation of modern ecosystems.

24 **Keywords:** Curlytail lizard, Extinction, Human Impact, Lesser Antilles, Osteology.

25 **Introduction**

26 The West Indies are known to have been severely impacted over the last several hundred to thousand  
27 years by both climatic and anthropogenic events that reshaped most of their biological diversity. The  
28 rich historical, archaeological, and paleontological records of these islands reveal hundreds of  
29 extinction events touching all taxa and regions (Cooke *et al.* 2017; Orihuela *et al.* 2020; Steadman *et*  
30 *al.* 2015). The causes underlying these extinctions have been the subject of considerable debate, as  
31 early research focused almost uniquely on the Pleistocene–Holocene transition as the main extinction  
32 factor (e. g. Pregill & Olson 1981; Underwood 1964). However, numerous recent work has  
33 demonstrated the considerable impact of human colonization and anthropization that led to the  
34 extinction of a relatively substantial portion of the local biodiversity (Bochaton *et al.* 2015b; Cooke *et*  
35 *al.* 2017; Soto-Centeno & Steadman 2015; Steadman *et al.* 1984, 2015). These studies also  
36 demonstrated the West Indies to be a perfect case study for exploring the long term impact of humans  
37 on island ecosystems in the framework of the current mass extinction crisis (Barnosky *et al.* 2011;  
38 Ceballos *et al.* 2015, 2017). Of the taxa impacted by these extinction events, several were almost  
39 completely wiped out from the Lesser Antilles. This group of strongly affected taxa comprises  
40 multiple squamates, including diploglossine lizards (Bochaton *et al.* 2015a, 2016), *Boa* snakes  
41 (Bochaton 2020; Bochaton & Bailon 2018) and leiocephalid lizards (Etheridge 1964; Pregill *et al.*  
42 1988) the latter, which despite being one of the few squamate genera endemic to the West Indies, still  
43 remains poorly understood. The monophyly of the *Leiocephalus* (Gray 1827) species restricted to the  
44 West Indies was documented in the 1960s (Etheridge 1966) and confirmed by molecular evidence  
45 (Pyron *et al.* 2013), with the members of this genus first included in their own subfamily and then  
46 family (Leiocephalidae Frost & Etheridge 1989). The genus *Leiocephalus* currently comprises 24  
47 species exclusively distributed in the Greater Antilles (Hedges 2020), including seven extinct species,  
48 five of which are known only from fossil remains (Pregill 1992). Among these extinct species, two  
49 were endemic to the Lesser Antilles, an area where no *Leiocephalus* species are currently known. The  
50 first of these species is *Leiocephalus herminieri* (Duméril & Bibron 1837), whose fluid-preserved type  
51 specimens were collected in Martinique during the 19<sup>th</sup> century (for a discussion concerning the origin  
52 of these specimens see Breuil -2002-). The second species is *Leiocephalus cuneus* Etheridge, 1964, a  
53 taxa that was originally described on the basis of fossil remains collected in Barbuda (Etheridge 1964;

54 Watters *et al.* 1984) but whose distribution was later extended to Antigua (Pregill *et al.* 1988), and  
55 possibly to Anguilla, La Désirade, and Marie-Galante (Bailon *et al.* 2015; Boudadi-Maligne *et al.*  
56 2016; Pregill 1992; Pregill *et al.* 1994; Stouvenot *et al.* 2014). The distribution of this taxon outside  
57 Barbuda and Antigua is however doubtful, as no clear fossil evidence is currently available. In  
58 Guadeloupe, the past occurrence of *Leiocephalus* lizards was mentioned in several historical texts  
59 (Breuil 2002; Du Tertre 1654; de Rochefort 1658) although their precise taxonomic identification is  
60 unclear. Historical data and biogeographic hypotheses all suggest that *Leiocephalus* may have  
61 previously been widespread in the Lesser Antilles. The current fossil record may therefore be  
62 substantially unrepresentative of the past diversity of this lizard. The phylogenetic relationships  
63 between both modern and fossil *Leiocephalus* species are also poorly understood. Until recently, the  
64 most comprehensive study of this genus concerned morphological characters combining both modern  
65 and known fossil taxa (Pregill 1992). However, none of the clades recognized in this pioneering work  
66 were confirming by the few non-exhaustive molecular analysis conducted since (Köhler *et al.* 2016;  
67 Pyron *et al.* 2013). In addition, both morphological and molecular analyses seem to indicate a complex  
68 colonization scenario comprising multiple colonization events. Overall, the history and past diversity  
69 of the genus *Leiocephalus* in the Lesser Antilles is poorly documented. For example, we currently do  
70 not know how these species were diversified in this area, where they came from, and when and why  
71 they went extinct. Here we provide important new descriptions of both historical and fossil specimens  
72 of *Leiocephalus* collected in Guadeloupe that we attribute to a new endemic species: *Leiocephalus*  
73 *roquetus* sp. nov.

## 74 **Materials and method**

### 75 Dry museum specimen

76 The holotype of *Leiocephalus roquetus* sp. nov. is a dry taxidermy specimen stored in the Natural  
77 History Museum of Bordeaux (MHNbx) in France. The specimen was donated to the museum around  
78 1835 by Théodore Roger (1784–1838), an alcohol manufacturer and naturalist better known for his  
79 collection of Lepidoptera. Very few details are available concerning the origin of the holotype

80 specimen; it is stored with a label reading “Holotropide de l’Herminier *Holotropis herminieri* Gray  
81 Guadeloupe donation Roger” with the species author’s name “*herminieri*” erroneously attributed to  
82 Gray, and “Guadeloupe” being the geographic origin of the specimen. This label is, in fact, a mid 20<sup>th</sup>  
83 century copy of the original 19<sup>th</sup> century label, and it is possible that some information originally  
84 attached to the specimen has been lost. The first catalog record to unambiguously mention this  
85 specimen under the name *Holotropis herminieri* Duméril & Bibron, 1837 comes from the beginning of  
86 the 20<sup>th</sup> century, suggesting that this specimen remained unidentified for years. The fact that the  
87 locality “Guadeloupe” contradicts the (erroneous) species identification (*Leiocephalus herminieri*  
88 being endemic to Martinique) is a clue that the origin was originally already attached to the specimen  
89 as it was not inferred from what is potentially a more recent taxonomic attribution. Although the  
90 general interest of this specimen was previously recognized (Breuil 2009), it remained unstudied until  
91 now.

## 92 Subfossil material

93 In addition to the specimen from the Natural History Museum of Bordeaux, more than 300  
94 *Leiocephalus* remains have been recorded from 31 different archaeological and paleontological  
95 deposits in Guadeloupe islands (Bochaton 2016). However, only a single deposit, Pointe Gros  
96 Rempart 6 (PGR6) on the island of La Désirade, yielded enough well-preserved bones to enable a  
97 formal evaluation, description, and identification of the *Leiocephalus* species they represent. While  
98 this site is still largely unpublished it nevertheless produced a noteworthy assemblage of squamate  
99 remains (Bochaton 2020; Bochaton *et al.* 2018), including 218 of the 320 *Leiocephalus* remains  
100 currently known from the Guadeloupe Islands. For this study, we compare the material from PGR6 to  
101 the dry specimen from Bordeaux, retaining only the most well-preserved fossil remains for  
102 description. We also integrated remains collected from other Guadeloupe islands, although no large,  
103 well-preserved fossil assemblages outside of La Désirade are currently available to identify them to  
104 species. The fossil bones from PGR6 are archaeological specimens and are therefore the property of  
105 the French state. Currently stored at the *Service Régional de l’Archéologie de Guadeloupe*, we plan to

106 petition for these bones described as paratypes to be united with the holotype dry-specimen in a single  
107 collection housed at the Natural History Museum of Bordeaux.

108 The site of Pointe Gros Rempart 6 (16819041.5600N, 6180049.1800W WGS84) is a pit cave situated  
109 on the coastal plain of La Désirade Island. This island was once connected to the other main islands of  
110 the Guadeloupe archipelago (Grande-Terre, Basse-Terre, and Petite-Terre) during the Pleistocene  
111 when sea levels were 100 meters lower (Fig. 1–A). PGR6 contains a stratified fossil-bearing deposit  
112 that has been the object of two excavations, the first in 2011 led by M. Boudadi-Maligne (Boudadi-  
113 Maligne *et al.* 2016), and the second in 2016 led by A. Lenoble. The still largely unpublished fossil  
114 assemblage from the more recent excavations produced 191 of the 218 *Leiocephalus* bones found from  
115 the site. The fossil material was collected during dry sieving in 2011 and subsequent wet sieving of the  
116 sediment using 2mm<sup>2</sup> mesh sieves in 2016. The sieved sediment was recorded by successive, 5cm  
117 thick horizontal spits (*décapages*) during excavations.

118 The 2016 excavations helped clarify the chronology of the four stratigraphic units identified during the  
119 initial work at the site (Fig. 1–B). An initial radiocarbon date obtained on a sample recovered during  
120 the 2011 excavations provided an age of 299-507 cal. AD for the base of the layer 3. Two additional  
121 radiocarbon dates, one on charcoal (Lyon-14287 –SacA-50616-) recovered from the base of layer 4  
122 (square B10d, *décapage* 22) provided a date of 170 BC – 4 cal. AD (2060±30 BP), the other on a  
123 Yellow-crowned night-heron bone (Lyon-14478 -SacA-51014-) from the top of the layer 3 (square  
124 B10d, *décapage* 11) produced a date of 1297-1373 cal. AD (600 ± 30 BP). These new dates are in  
125 good agreement with the initial chronological interpretation of the stratigraphy based on the  
126 archaeological material (pottery sherds and bones of introduced species). Layer 1 has been attributed  
127 to modern activity over the last 200 years, layer 2 to the Colonial period, and layers 3 and 4 to the pre-  
128 Columbian Ceramic period between around 200 BC and 1728 AD. The pre-Columbian Ceramic era is  
129 divided into different sub-periods spanning from 80 AD to around 1600 AD in Guadeloupe  
130 (Fitzpatrick 2015; Hofman *et al.* 1999; Keegan *et al.* 2013) and to 1728 AD in La Désirade (Boudadi-  
131 Maligne *et al.* 2016). The few ceramic remains recovered from PGR6 do not provide any additional  
132 chronological resolution ( for details see Boudadi-Maligne *et al.* 2016).

133

134 CT-scanning

135 We produced high-resolution 3D models of the head of the dry specimen from the Bordeaux Natural  
136 History Museum in order to describe its skull morphology without damaging the specimen. Micro-CT  
137 imaging was performed using a GE v|tome|x s  $\mu$ CT scanner at the UMS 3626 PLACAMAT laboratory  
138 of the University of Bordeaux (France) with acquisition parameters set to 100 kV (tension), 200  $\mu$ A  
139 (Intensity), and 333 ms (exposure time) for a total of 2550 projections. A 0.1 mm copper filter was  
140 used to reduce beam hardening artifacts. The geometry was set to obtain a 13.7  $\mu$ m voxel size in the  
141 reconstructed three-dimensional images. The reconstruction was generated using the phoenix datos|x  
142 v. 2.2.1.716 scanning software. Each bone of the specimen was manually segmented and  
143 individualized by creating a sub-set of selected voxels in AVIZO v. 9.3 (VSG, SAS, Merignac,  
144 France, <http://www.vsg3d.com>). This final manipulation was impossible to perform automatically  
145 given the presence of a metallic rod within the head of the specimen, which produced visual artifacts  
146 that we had to remove manually.

147 Phylogenetic analysis

148 Phylogenetic analysis was conducted using the characters and character matrix of Pregill (1992),  
149 completed with the data we collected from the dry specimen and fossil bones from Guadeloupe. The  
150 theoretical ancestor of Pregill (1992) was included in the analysis but, as it included undetermined (?)  
151 character states, we incorporated two additional “ancestors” with either 0 or 1 character states as out-  
152 group taxa. The most parsimonious trees were determined from the obtained matrix (Appendix 1)  
153 using a parsimony branch and bound search with the PAUP4 v.3.99.167.0 software  
154 (<https://paup.phylosolutions.com>). We then computed a consensus of the trees obtained.

155 Anatomical descriptions

156 The description of the external anatomy of the Holotype follows the same terminology as Pregill  
157 (1992). The osteological description mostly follow the nomenclature Fejérvary-Langh (1923) and

158 Evans (2008). This terminology was complemented by other references (Bailon 1991; Klembara *et al.*  
159 2010; Oelrich 1956; Smith *et al.* 2018), some of which are mentioned in the text when needed.

160

## 161 **Results**

162 Comparison of both the dry specimen from the Natural History Museum of Bordeaux (MHNbX) and  
163 the fossil remains from Guadeloupe with existing data concerning the morphology of known  
164 *Leiocephalus* species indicates the Guadeloupe specimens to bear both unique morphological  
165 characters and combinations of morphological characters that exist in no other known *Leiocephalus*  
166 species. As such, we have attributed the Guadeloupe specimens to a new species, *Leiocephalus*  
167 *roquetus* sp. nov., for which we provide a formal description and complete diagnosis.

168 *Leiocephalus roquetus* sp. nov.

169 Fig. 2, 3,4,5,6, 7

170 **Diagnosis.** *Leiocephalus roquetus* differs from all other congeners by the morphology of its parietal  
171 bone that bears adductor crests fused into a single crest in the posterior area of the bone in large  
172 specimens. In addition of this character, *L. roquetus* presents a unique combination of characters:  
173 absence of enlarged snout scales, and occurrence of five scales in contact with the first pair of enlarged  
174 frontal scales (pattern of type I of Pregill (1992)), the occurrence of three internasal scales, a  
175 prominent dorsal body crest, absence of keeled ventral scales, frontal bone exposed dorsally between  
176 the nasal and prefrontal bones, skull rugosities on the frontal bone, premaxillary spine constricted just  
177 above the dentigerous process, a well-developed posterior process of the septomaxilla, a distinct dorsal  
178 process of the squamosal, a well-developed angular process of the dentary, and transition from  
179 bicuspid to tricuspid teeth occurs between the height and sixth most anterior dental position of the  
180 dentary. This new taxon also presents several differences with other known Lesser Antillean  
181 *Leiocephalus* specimens (see below).



182 **Derivatio nominis:** The species is named in reference to the first common name “roquet” attributed  
183 by Du Tertre (1654) and de Rochefort (1658) to the leiocephalid lizards of Guadeloupe. As pointed  
184 out by Breuil (2002), this name was latter erroneously attributed to *Anolis* lizards and, as the  
185 Amerindian name of *Leiocephalus* is unknown, we choose to retain the original name given to these  
186 squamates. The English name of this lizard would be “Curlytail roquet” and the French name  
187 “Léiocéphale roquet”.

188 **Type locality:** Guadeloupe, ? La Désirade Island, Lesser Antilles.

189 **General description of the holotype.** The holotype is a complete, dry taxidermy specimen (labeled  
190 MHNbx 2002.1871) preserved in the Natural History Museum of Bordeaux (France). This specimen  
191 has a snout-vent length (SVL) of 10.8 cm and measures 26.5 cm in total length (Fig. 2).  
192 Microtomography reveals the skull to be fully preserved (Fig. 3). The key morphological features of  
193 the holotype are as follows: enlarged nasal bones, the narrow nasal process of the premaxilla is  
194 triangular, the dorsal part of the premaxilla is fully enclosed by the nasal bones, the premaxilla lacks  
195 lateral spines and bears 7 tooth positions, the nasal-maxillary suture is arched toward the mid-line of  
196 the snout, the nasal process of the frontal bone is dorsally exposed between the nasal and prefrontal  
197 bones, the pterygoid bears teeth but palatine teeth are absent, lacrimal and postfrontal bones are  
198 present, the septomaxilla bears a quadrangular lateral wing with a thin posteriorly oriented process, the  
199 frontal is narrow with dermal ornamentation, the parietal foramen is on the fronto-parietal suture, the  
200 adductor crests of the parietal table converge but do not touch and are posteriorly separated by a  
201 depressed area, the anterior part of the parietal table presents a dermal ornamentation, the  
202 supratemporal bone is on the lateral side of the supratemporal process of the parietal, the  
203 supratemporal process of the squamosal is distinct, splenial and angular bones are present, the angular  
204 process of the dentary is well-developed, most of the teeth are tricuspid and distinctively flared, the  
205 transition from monocuspid/bicuspid to tricuspid teeth occurs at the seventh dental position on the  
206 dentary and at the fourth dental position on the maxilla. Head scales are large, the specimen presents  
207 four rows of snout scales of sub-equal size between the internasal and the anterior pair of frontal  
208 scales, there are four moderately-sized parietal scales and the most lateral scales are smaller than the

209 median scales, two rows of post parietal scales are present, there is no enlarged lateral post-parietal  
210 scale, there are three internasal scales, there are four lorilabial scales anterior to the first lorilabial  
211 contacting the elongated sub-ocular scale, the cephalic scales lack ridges, the temporal scales are of  
212 sub-equal size and no elongated temporal scales are present, the lateral nuchal scales are smaller than  
213 surrounding body scales, the lateral body scales are the same size as dorsal and ventral scales, a  
214 prominent middorsal body crest formed by overlapping scales is present, the dorsal crest (occiput to  
215 vent) is composed of 53 scales, the tricarnate scales at the base of the first and second toes grow into  
216 comb-like fringes but are not prominent, the venter is dull and patternless, there is no scapular patch,  
217 no suprascapular blotches, no facial band, and the base of tail is laterally compressed.

218 **Description of paratype fossil bones and corresponding bones of the holotype.** In addition to the  
219 holotype dry specimen, we associate, as paratypes, several fossil bones collected from the Pointe Gros  
220 Rempart 6 deposit to the type series of *L. roquetus*. These bones are described below in association  
221 with corresponding bones of the holotype specimen in order to demonstrate that both modern and  
222 fossil materials correspond to the same taxon.

### 223 **Premaxilla**

224 **Holotype** (MHNbx 2002.1871) (Fig. 4–A): The premaxilla is a single bone and measures 2.8 mm  
225 across the rostrum. In posterior view, the supradental shelf tends to extend moderately both laterally  
226 and posteriorly. In anterior view, the bone presents a single incisive process oriented ventrally,  
227 reaching half the height of the maxillary process. The nasal process is high and triangular with the  
228 thinner dorsal part fully covered by imprints of the nasal bones. The portion of the nasal process that is  
229 not covered by the nasal bones on the articulated skull is triangular with a slight constriction at the  
230 base. The nasal process lacks lateral spikes *sensu* Pregill (1992). The imprints of the maxilla are  
231 weakly extended on the lateral side of the maxillary processes (lateral processes *sensu* Oelrich 1956).  
232 The bone bears seven tooth positions occupied by conical, monocuspid pleurodont teeth. The  
233 morphology of these teeth cannot be further described as the majority are broken, probably during the  
234 preparation the specimen.

235 **Paratype** “PGR6. square C11c. *décapage* 14.XII” (Fig. 4–B): This element is a complete subfossil  
236 premaxilla collected from layer 3 of PGR6 (square C11c; *décapage* 14). This element measures 4.2  
237 mm across the rostrum. This bone is similar to the holotype and allows further detail to be described  
238 for the morphology of the teeth, which are monocuspid, blunt, and slightly pointed on this specimen.  
239 As in the holotype and every premaxilla from PGR6, this element does not exhibit any dermal  
240 ornamentation.

241 Additional material: Two additional well-preserved premaxillas were recovered from the PGR6  
242 deposit and are identical to the holotype and paratype described above. The teeth preserved on these  
243 bones are all monocuspids.

#### 244 **Maxilla**

245 **Holotype** (MHNbx 2002.1871) (Fig. 4–C): The bone bears a 12 mm long dental row bearing 21 tooth  
246 positions. The most anterior tooth is conical, the second and third are bicuspid with a large posterior  
247 cusp and a reduced anterior cusp. The following teeth are tricuspid (with a dominant central cusp),  
248 linguolabially compressed, distinctively flared in mesio-distal direction. The shape of these teeth is  
249 similar to that of tricuspid teeth of the dentary (see below). In medial view, the supradental shelf (  
250 *sensu* Rage & Augé 2010) is slightly arched toward the mid-length of the bone. The facial process is  
251 triangular, longer than it is high. The posterior process is short, and is in equivalent in length to the  
252 portion of the supradental shelf bearing the two last dental positions, and its posterior tip is  
253 quadrangular in dorsal view. In labial view, the antero-dorsal margin of the facial process is strongly  
254 inflected medially. The surface of the facial process is punctuated by several small foramina, and six  
255 larger labial foramina are present. The bone lacks dermal ornamentation. In dorsal view, the  
256 supradental shelf is triangular. The internal premaxillary process is more developed than the external  
257 one. This process is high and thin, and its antero-dorsal margin is linked to the medial margin of the  
258 facial process by a crest visible in medial view. A moderately deep V-shaped premaxillary fenestra  
259 separates the internal and external premaxillary processes.

260 **Paratype** “PGR6. square B10d. *décapage* 22.III” (Fig. 4–D): This element is a complete subfossil  
261 maxilla recovered from layer 4 of PGR6 (square B10d; *décapage* 22). This bone, although similar to  
262 the holotype, nevertheless presents several differences. This maxilla has a 15.4 mm long dental row  
263 with 22 tooth positions. The most anterior tooth is bicuspid and the most anterior tricuspid tooth  
264 occupies the fifth tooth position.

265 Additional material: Six additional, well-preserved maxillae were recovered from the PGR 6 deposit.  
266 These bones are similar to those described above but present variable numbers of tooth positions,  
267 ranging between 17 for the smallest specimens (dental row length = 9 mm) to 22 for the largest  
268 individuals (dental row = 13.56–16.3 mm). The most anterior tricuspid tooth of these specimens  
269 appears at the fourth or fifth tooth position.

## 270 **Frontal bone**

271 **Holotype** (MHNbx 2002.1871) (Fig. 5–A): The two frontal bones are fused (azygous). In dorsal view,  
272 the bone is elongated, 2.5 times wider in its posterior than in its anterior part, with a nearly straight  
273 parietal margin. The minimal width of this element at the level of its median constriction is 3.1 mm.  
274 The bone exhibits a moderately marked tuberculated dermal ornamentation on the entire dorsal surface  
275 of the bone. The parietal foramen is present at the posterior end of the bone and partially opens onto  
276 the fronto-parietal suture. In dorsal view, the anterior end of the bone presents deep imprints of the  
277 nasal bones. Nasal and prefrontal bones are independent in the anterior area of the frontal, as  
278 demonstrated by the occurrence of two well-marked crests on the nasal process separating imprints of  
279 the nasal and prefrontal bones. In ventral view, the cranial crests (= *crista cranii*) are well  
280 individualized but are not prominent, and are independent of in the median area of the bone. The  
281 postfrontal bone imprint is visible at the anteromedial base of the posterolateral processes. Nearly the  
282 entire anterior half of the lateral margin of the bone is occupied by an imprint of the prefrontal bone,  
283 which is fully visible only in lateral view.

284 **Paratypes** “PGR6. square B10d. *décapage* 13.IV” (Fig. 5–B), and “PGR6. square B10d. *décapage*  
285 13.V” (Fig. 5–C): These bones were both found in layer 3 of PGR6 (square B10d, *décapage* 13) and

286 correspond to a large individual with a minimal width of 4.9 mm and a small specimen, probably a  
287 juvenile, with a minimal width of 2.2 mm. These specimens are morphological similar to the holotype.

## 288 **Parietal bone**

289 **Holotype** (MHNbX 2002.1871) (Fig. 5–D): The parietal bone is a single element and has maximal  
290 antero-posterior length of 9.5 mm. In dorsal view, the medial area of the bone is slightly laterally  
291 constricted . A slight central depression of the fronto-parietal suture of the bone indicates the position  
292 of the parietal foramen whose posterior margin is delimited by the parietal. The adductor crests are  
293 low and tend to converge posteriorly but are parallel in the posterior part of the bone. In the anterior  
294 part of the bone these crests delimit a U-shape, heavily ornamented area comprising elongated  
295 tubercles. In the posterior part of the bone, the adductor crests are separated by a slight postero-medial  
296 depression. The supratemporal processes are well individualized and extend posteriorly. Deep and  
297 clearly distinct nuchal fossae are present on the medial side of both supratemporal processes. These  
298 fossae are separated medially by a small longitudinal crest overlying the parietal fossa (recessus  
299 processi ascendentis *sensu* Smith (2011)). In lateral view, an imprint of the supratemporal bone covers  
300 the full length of the supratemporal processes.

301 **Paratypes**: “PGR6. square C11d. *décapage* 12.VI” (Fig. 5–E): This bone was found in layer 3 of  
302 PGR6, (square C11d, *décapage* 12). This element is a small medial fragment of a parietal bone,  
303 similar in size to the holotype. The morphology of this element is similar to the holotype, including the  
304 occurrence of weakly defined adductor crests separated by a small depression in the posterior part of  
305 the bone.

306 “PGR6. square B9b. *décapage* 22.VII” (Fig. 5–F): This bone was found in layer 4 of PGR6 (square  
307 B9b, *décapage* 22). This element is a nearly complete parietal in a more advanced ontogenetic stage  
308 than the holotype and paratype described above. It is larger than the other parietal bones we identified,  
309 with a maximal antero-posterior length of 12.3 mm. While similar to the holotype, the morphology of  
310 the parietal table and adductor crests is completely different. In addition to being high and well

311 defined, the crests delimit a V-shape ornamented area and meet in the posterior part of the bone to  
312 form a single crest reaching the postero-median extremity of the parietal table.

313 Specific remarks regarding the attribution of the paratype “PGR6. square B9b. *décapage* 22.VII” to  
314 *Leiocephalus roquetus*: The morphology of this element is substantially different from the holotype,  
315 leading us to explore whether it formed part of the morphological variability of the same taxa or  
316 reflects a different species. This is all the more important considering that the morphology of this  
317 particular parietal bone differs from all known *Leiocephalus*. The attribution of the paratype “VII” to  
318 *Leiocephalus* is however supported by its numerous similarities with the holotype, including the  
319 overall shape of the bone, the morphology of the supratemporal processes and parietal fossae, the  
320 absence of parietal foramen, and the occurrence of a well-delimited ornamented area in the antero-  
321 medial area of the bone. In addition, similar ontogenetic parietal morphological variability exists in  
322 several other pleurodont squamates (e. g. *Anolis* -Bochaton *et al.* 2017-, *Iguana* -Bochaton *et al.* 2019-  
323 ) including *Leiocephalus* itself (Pregill 1992) although the adult morphology usually differs from our  
324 paratype “VII”. However, the adductor crests in *Leiocephalus* usually converge in the posterior area of  
325 the bone. We included this bone in the morphological variability of *L. roquetus* given the occurrence  
326 of the smaller parietal paratype “VI”, similar to the holotype, in the same deposit, which reinforces our  
327 interpretation of paratype “VII” representing an older specimen with a more ontogenetically advanced  
328 morphology.

### 329 **Pterygoid bone**

330 **Holotype** (MHNbx 2002.1871) (Fig. 6–A): The bone presents a long, thin posterior process  
331 accounting for half of the length of the complete bone. In dorsal view, the transverse process extends  
332 moderately laterally and bears a well-marked, triangular articular surface with the ectopterygoid. The  
333 base of the posterior process has a deep pit for the insertion of the epipterygoid bone. In dorsal view,  
334 the palatine process forms a long and relatively thin blade whose pointed anterior tip bears a well-  
335 defined contact area with the palatine bone. In medial view, the anterior extremity of the posterior  
336 process presents a deep indentation occupied by a well-marked articular surface for the basipterygoid

337 process of the basisphenoid bone. Posteriorly to this structure, an oval pterygoid furrow occupies most  
338 of the medial area of the posterior process. In ventral view, the palatal process present superficial  
339 traces of teeth sockets (*sensu* Mahler & Kearney 2006), and two teeth were present on the left  
340 pterygoid of the holotype specimen. However, these teeth were not attached to the bone by any  
341 ossified structure and were absent on the right pterygoid. It is therefore difficult to be certain if the  
342 absence of pterygoid teeth is a general trait of *L. roquetus* as this character could reflect intra-  
343 individual and intra-specific variability. Such variability was previously observed by Mahler &  
344 Kearney (2006) in the genus *Leiocephalus*.

345 **Paratypes:** “PGR6. square C11d. *décapage* 14.X” (Fig. 6–B): This bone, recovered from layer 4 of  
346 PGR6 (square C11d, *décapage* 14), is similar to the holotype but it lacks any trace of teeth sockets.  
347 Instead, the anterior part of the palatal process bears two short bulbous processes of unknown nature in  
348 places that would normally be occupied by teeth. We are unable to determine whether these processes  
349 are teeth or bony formations. The morphology of the palatal process displays some variability in the  
350 PGR6 fossils. This process can be more or less depressed and usually lacks teeth-related structures,  
351 although the smallest fossil does present a single small bulbous process similar to those previously  
352 evocated. Considering that the holotype pterygoid is much smaller than any of the fossil pterygoid  
353 from PGR6, we assume that the occurrence of teeth on the pterygoid in *L. roquetus* may reflect  
354 ontogenetic or individual variability.

### 355 **Squamosal bone**

356 **Holotype** (MHNbx 2002.1871) (Fig. 6–C): In lateral view, the bone presents a long, narrow anterior  
357 ramus and two shorter posterior processes. The dorsal process (supratemporal process) is three times  
358 longer than the ventral process (quadrate process) and is clearly distinct. The tip of this process is  
359 rounded and the whole process is slightly oriented anteriorly. The ventral process is reduced and  
360 pointed.

361 **Paratypes:** “PGR6. square B9b. *décapage* 22.IX” (Fig. 6–D): This bone was found in layer 4 of PGR6  
362 (square B9b, *décapage* 22). This bone, while similar to the holotype, is larger and presents a clearly  
363 more developed ventral process. The ventral process is broken.

#### 364 **Septomaxilla**

365 The septomaxillae of the holotype are very thin which make difficult to observe their morphology in  
366 detail using the CT-scan data and to capture good images of it. We were however able to observe the  
367 main components of its morphology that are describe hereinafter. This bone was not found in the fossil  
368 material.

369 **Holotype** (MHNbx 2002.1871) (not figured): The septomaxilla presents a well-developed blade-like  
370 posterior process and a flat well-extended triangular anterior process 1.5 times longer than wide. The  
371 dorsal surface of this process is slightly concave. The septal process is poorly developed.

372

#### 373 **Quadrate bone**

374 **Holotype** (MHNbx 2002.1871) (Fig. 6–E): The bone is 5 mm high and sub-rectangular in anterior and  
375 posterior views. In posterior view, it is divided into two asymmetrical portions by a posterior crest.  
376 The lateral region is the most developed and comprises a deep conch delimited by a tympanic crest.  
377 This region is dorsally notched to receive the ventral process (quadrate process) of the squamosal. The  
378 medial region has a weakly-developed pterygoid lamina whose width is similar to or slightly thinner  
379 than the posterior crest. In anterior view, the dorsal part of the tympanic crest region is occupied by a  
380 weakly marked antero-dorsal depression.

381 **Paratypes:** “PGR6. square C11c. *décapage* 15.XI” (Fig. 6–F): This bone comes from layer 3 of PGR6  
382 (square C11c, *décapage* 15). This bone is similar to the holotype but is larger (7.7 mm high) and its  
383 antero-dorsal depression is more strongly marked and delimited than in the holotype which could  
384 reflect ontogenetic variability.

#### 385 **Dentary**



386 **Holotype** (MHNbx 2002.1871) (Fig. 7–A): The bone is straight and elongated. Its dental row is 13  
387 mm long and bears 25 teeth. The six most anterior teeth positions bear simple mono-pointed conical  
388 teeth, remaining teeth are tricuspid, linguolabially compressed, distinctively flared in mesio-distal  
389 direction, and present large and pointed secondary cusps. In lateral view, the symphysis is thin and  
390 oblong. The surangular and angular processes are well-developed and extend posteriorly well beyond  
391 the level of the dental row. The surangular process extends posteriorly well beyond the apex of  
392 coronoid. The angular process is more pointed than the surangular process, which is blunter and  
393 shorter. Its length is equivalent to two-thirds the surangular process. The dentary also presents a well-  
394 individualized coronoid process extending inside the coronoid bone in the complete mandible. An  
395 intra-mandibular septum is presents below the dental row, between the last and fourth-to-last dental  
396 positions. An intramandibular lamella (*sensu* Smith 2009) is present and well-developed. In medial  
397 view, a large imprint of the anteromedial process of the coronoid bone is visible on the posterior  
398 extremity of the bone and extends below the three last dental positions of the dental row. In ventral  
399 view, the Meckelian groove is nearly fully enclosed by the dorsal and ventral flanges of the dentary  
400 that are fully fused on the three-quarters of the length of the dental row. The anterior extremity of the  
401 Meckelian groove remains open by a slender opening below the first to seventh most anterior tooth  
402 positions.

403 **Paratypes**: “PGR6. square C11d. *décapage* 16.I” (Fig. 7–B): This bone is a nearly complete subfossil  
404 dentary missing only its posterior extremity. This bone was recovered from layer 3 of PGR6 (square  
405 C11d; *décapage* 16). This bone is similar to the holotype however the most anterior tricuspid tooth  
406 appears at the 8<sup>th</sup> tooth position. It also bears less dental positions (n=21) due to its shorter dental row  
407 (14.6 mm). The anterior opening of the Meckelian groove is also less posteriorly extended than on the  
408 holotype as it extends only below the five most anterior dental positions.

409 “PGR6. square C11c. *décapage* 11.II” (Fig. 7–C): This bone is a nearly complete subfossil dentary  
410 missing its posterior extremity and whose anterior part is dissolved, probably due to it being digested  
411 just as several other bone remains in the fossil assemblage presenting characteristic marks of digestion  
412 (Fernández-Jalvo & Andrews 2016). This bone was also found in layer 3 of PGR6 layer (square C11c;

413 *décapage* 11) and exhibits a similar dental length (14.4 mm) and number of teeth (n=25) to the  
414 holotype.

415 Additional material: Two additional but less well-preserved dentaries were also recovered from PGR6.  
416 Dental rows measure 14.7 mm and 12 mm and bear, respectively, 21 and 20 tooth positions. The  
417 smallest dentary presents a juvenile morphology and the most anterior tricuspid tooth occupies the  
418 sixth most anterior tooth position.

#### 419 Articular

420 **Holotype** (Fig. 7–D): In dorsal view, the elongated articular is four times longer than wide with well-  
421 developed articular and retroarticular processes. The articular process is triangular with a medially  
422 oriented apex. The retroarticular process is rectangular and separated from the articular process by a  
423 well-marked ridge. The articular process extends 2 mm medially from the medial border of the  
424 condyle.

425 **Paratype**: “PGR6. square B9b. *décapage* 17.VIII” (Fig. 7–E): This element was recovered from layer  
426 3 of PGR6 (square B9b, *décapage* 17) and comprises complete and fused articular and surangular  
427 bones. The retroarticular process is almost square in dorsal view. The articular process is similar to  
428 that of the holotype but is more extended medially. The limit between the articular and the  
429 retroarticular processes is not marked by any structure and is therefore difficult to delimit. The  
430 articular process extends 4.1 mm medially from the medial border of the condyle.

431 Specific remarks regarding the morphological variability of the articular bone: The holotype and the  
432 largest articular bone found from PGR6 (Paratype “PGR6. square B9b. *décapage* 17.VIII”) differ  
433 somewhat in regards the morphology of the articular and retroarticular processes. These processes are  
434 widened medially in the largest specimen, and the limit between the two processes becomes  
435 indistinguishable. As other pleurodont squamate genera display a similar degree morphological  
436 variability, we interpret this difference as reflecting ontogenetic variability in *Leiocephalus roquetus*.

437 Additional remarks regarding fossil post-cranial elements:

438 In addition of the cranial elements described above, the PGR6 deposit produced several postcranial  
439 elements of *Leiocephalus* that we attribute to *L. roquetus*. However, as comparing these elements with  
440 the holotype specimen was impossible, we describe their main morphological characters without  
441 considering these bones as type material.

442 **Dorsal Vertebrae:** We attributed forty-seven dorsal vertebrae recovered from PGR6 to *Leiocephalus*  
443 *roquetus*. The morphology of these vertebrae varies depending on their position on the vertebral  
444 column, as indicated by the morphology of the synapophyses. One of the most significant differences  
445 is the morphology of the hypapophysis, which is narrow and forms a longitudinal ridge in cervical and  
446 anterior trunk vertebrae and becomes uniformly wide and flat in median and posterior trunk vertebrae.  
447 However, all complete vertebrae, independent of their position on the column, present a high, vertical  
448 neural spine (Fig. 7–F). This combination of characters is typical of most *Leiocephalus* species (Pregill  
449 1992).

450 **Caudal vertebrae:** The ten caudal vertebrae recovered from PGR6 present a slender medial spine  
451 projected vertically above the neural arch at the position of the fracture plane. This character is an  
452 apomorphy in *Leiocephalus* (Etheridge 1966; Pregill 1992).

453 **General remarks:**

454 The diagnosis of *L. roquetus* is based on a combination of a single historical dry-specimen (holotype)  
455 and fossil bone remains (paratypes) sharing common anatomical characteristics and likely  
456 geographical origin. Both of these types of material would have independently led to the same  
457 conclusion (the description of a new species) but the combined information they provide allow for a  
458 complete assessment of the external morphology and osteological ontogenetic variability of *L.*  
459 *roquetus* sp. nov. The combined consideration of the holotype juvenile dry-specimen and the  
460 paratypes fossil remains from PGR 6 is enabled by the strict osteological similarity between these  
461 materials as it is demonstrated by our cladistic analysis.

462 *L. roquetus* presents a combination of characters shared with *L. herminieri* from Martinique, which  
463 would place it in a hypothetical Lesser Antillean clade (see below): the absence of enlarged snout

464 scales and the occurrence of five scales in contact the first pair of enlarged frontal scales (the type I  
465 pattern of Pregill -1992-), frontal bone exposed dorsally between the nasal and prefrontal bones, skull  
466 rugosities on the frontal bone, and a prominent dorsal body crest. The fossil species *L. cuneus* from  
467 Antigua bears the two osteological characters shared between *L. roquetus* and *L. herminieri*, however,  
468 as these characters also occur in Greater Antillean taxa, it is impossible to link *L. cuneus* to a putative  
469 Lesser Antillean clade. Moreover, such a hypothesis is not supported by our phylogenetic analysis (see  
470 below).

471 Although potentially forming part of the same clade, *L. roquetus* presents several morphological  
472 differences with the two other *Leiocephalus* described in the Lesser Antilles in addition to the  
473 morphology of its parietal bone.

474 - with *L. herminieri*: absence of keeled ventral scales, occurrence of three internasal scales,  
475 premaxillary spine constricted just above the dentigerous process, occurrence of well-developed  
476 posterior process of the septomaxilla, occurrence of a distinct dorsal process of the squamosal,  
477 occurrence of a well-developed angular process of the dentary, the most anterior occurrence of  
478 tricuspid teeth between the 6<sup>th</sup> and the 9<sup>th</sup> most anterior dental position of the dentary.

479 -with *L. cuneus*, the only other fossil *Leiocephalus* described in the Lesser Antilles and whose past  
480 occurrence was suspected in Guadeloupe: absence of bicuspid teeth on the premaxilla, absence of  
481 dermal ornamentation on the premaxilla, premaxillary spine constricted just above the dentigerous  
482 process, occurrence of “teeth” on the pterygoid bones of some specimens, absence of tricuspid teeth on  
483 the 4<sup>th</sup> and 5<sup>th</sup> dental positions of the dentary, absence of a V-shaped indentation separating the angular  
484 from the retroarticular process of the articular bone.

485 In terms of the size of *L. roquetus*, although the holotype specimen is moderate in size (snout-vent  
486 length of 10.8 cm), most of the fossil bones attributed to this species were larger, indicating that the  
487 type specimen is likely to be a juvenile. Isolated bones do not, however, provide direct evidence for  
488 the size of the complete specimen, and we can only provide a rough estimate of the putative size of  
489 adult *L. roquetus*. The fossil bones from PGR6 are of similar size to the largest bones reported by R.

490 Etheridge (1964) to estimate the size of *L. cuneus* (200 mm SVL). Certain elements are both smaller  
491 (premaxilla, quadrate, dentary, articular) or larger (maxilla, frontal, parietal), leading us to estimate *L.*  
492 *roquetus* to be roughly of similar size as *L. cuneus*, which is currently the largest known *Leiocephalus*  
493 species.

#### 494 **Phylogenetic relationships of *L. roquetus* in regard to other *Leiocephalus* species**

495 To complement our morphological analysis of *L. roquetus*, we placed this newly described taxon in  
496 the only available morphological phylogeny of *Leiocephalus* (Pregill 1992). The parsimony analysis  
497 generated 177 optimal trees of 130 steps (Consistency Index -CI- =0.408 and Retention Index -RI-  
498 =0.603). We then computed the consensus of these trees (Fig. 8). Our parsimony analysis produced  
499 almost exactly the same results as those reported by Pregill (1992) with similar data (CI=0.441,  
500 RI=0.590). The addition of additional ancestors did not modify the topology of the tree obtained by  
501 Pregill (1992). The basal position of *L. herminieri* inferred by Pregill (1992) in regard to other  
502 *Leiocephalus* is partly confirmed by our analysis but this part of the tree is more poorly resolved than  
503 that of the previous study. Our newly described *L. roquetus* appears to be the closest relative of this  
504 also extinct, taxon. Our results indicate the existence of a putative but now completely extinct Lesser  
505 Antillean clade, which might reflect an individual colonization event of the Lesser Antilles that may  
506 predates the colonization of the Greater Antilles. This hypothesis could be seen as in contradiction  
507 with the position of *L. cuneus*, which is not part of this putative Lesser Antillean group despite having  
508 been described in this area (primarily Antigua and Barbuda). This could be explained either by the low  
509 number of characters it was possible to record on *L. cuneus* due to the fact that only part of its  
510 osteology and none of its external morphology is currently known. However, we also performed a  
511 second analysis treating the complete holotype specimen and the fossil paratypes of *L. roquetus*  
512 independently (CI=0.405, RI=0.608). This analysis confirmed the holotype and paratype specimens to  
513 be more closely related to each other than to any other taxon and that *L. cuneus* was not part of that  
514 clade. There is thus also a possibility that *L. cuneus* has a Greater Antillean origin and is related to a  
515 different colonization event. However, the paucity of available fossil data makes it impossible to  
516 explore this question further.

## 517 **The past biodiversity of *Leiocephalus* in the Guadeloupe Islands**

518 Fossil evidence complemented by the historical specimen presented here allow us to describe an  
519 endemic and recently extinct species of *Leiocephalus* from Guadeloupe, whose past distribution in  
520 Guadeloupe remains unclear. *L. roquetus* was definitely present on La Désirade, which forms part of  
521 an island group comprising Grande-Terre, Basse-Terre, and Petite-Terre. This could suggest that these  
522 islands were occupied by a single species, as is generally the case for Lesser Antillean squamate taxa  
523 (Henderson & Powell 2009). However, the exact geographic origin of the type specimen of *L.*  
524 *roquetus* is unclear, and fossil occurrences of *Leiocephalus* are extremely rare in Guadeloupe. The  
525 occurrence of *L. cuneus* in Guadeloupe (Grande-Terre and La Désirade) had been previously  
526 suggested based uniquely on a small sample of fossil dentary bones on which the most anterior  
527 tricuspid tooth appears in the fifth most anterior dental position (Pregill 1992; Pregill *et al.* 1994). In  
528 addition to this material not be available for study, the lack of well-preserved *Leiocephalus* remains in  
529 the archaeological records of Grande-Terre and Basse-Terre makes evaluating this possibility difficult  
530 (Bochaton 2016). However, a premaxilla reported by Bochaton (2016) from the archaeological site of  
531 Anse à la Gourde (Grande Terre) lacked both bicuspid teeth and the dermal ornamentation typical of  
532 *L. cuneus*. The taxonomic identity of the *Leiocephalus* species which inhabited the main Guadeloupe  
533 islands therefore remains an open question. Regarding the putative occurrence of *L. cuneus* on La  
534 Désirade, we restudied the dentary described by Boudadi-Maligne *et al.* (2016). Our analysis found  
535 that the most anterior tricuspid tooth of this bone appears on the sixth and not on the fifth most  
536 anterior dental position, as initially reported, making it similar the dentary of *L. roquetus*. Regarding  
537 Marie-Galante, despite its rich fossil record, *Leiocephalus* remains are extremely rare in the  
538 archeological and paleontological deposits. The few available bones all have the most anterior  
539 tricuspid tooth on the fifth most anterior dental position on the dentaries (Stouvenot *et al.* 2014;  
540 Bochaton pers. obs.), a trait absent from *L. roquetus*. However, the unpublished premaxilla from Cadet  
541 3 on Marie-Galante (Bochaton pers. obs.) lacks bicuspid teeth and the dermal ornamentation typical of  
542 *L. cuneus* , making it impossible to definitively attribute it to this species. In the end, while we can be

543 certain that *L. roquetus* previously inhabited La Désirade, the fossil material is too scarce to identify  
544 fossils from the other islands of Guadeloupe to specific taxa.

## 545 **Discussion**

546 Our works add a third species to the list of now-extinct Lesser Antillean *Leiocephalus*. This very low  
547 species count compared to other Lesser Antillean lizards, especially anoles, is likely to be a heavy  
548 under-representation of the real past diversity of these lizards.

### 549 Causes and timing of the extinction of *Leiocephalus* in the Lesser Antilles

550 While the extinction of *Leiocephalus* during the colonial period in Guadeloupe was previously  
551 suggested by archaeological evidence (Bochaton 2016), the specimen housed at the Natural History  
552 Museum of Bordeaux, collected in the first half of the 19<sup>th</sup> century, adds more precision to the last  
553 occurrence date of this lizard. An early 19<sup>th</sup> century extinction of this lizard would be consistent with  
554 the last mention of *Leiocephalus* in Martinique, demonstrating the species to have disappeared from  
555 both islands only very recently. The potential causes underlying these extinctions could be the same as  
556 those frequently advanced for squamates: the impact of introduced mammalian predators (Henderson  
557 1992; Lorvelec *et al.* 2007), human-induced changes to landscapes and intensive agricultural practices  
558 (Boudadi-Maligne *et al.* 2016; Corke 1992), or a combination of several of these factors (Iverson  
559 1978). The general causes for the regional extinction of *Leiocephalus* are far from clear. This genus  
560 was probably among the most heavily impacted squamate genera, as it is the only genus that was  
561 completely wiped out from the Lesser Antilles sometime after the Late Pleistocene. The second most  
562 impacted genera, *Boa* and *Diploglossus*, also present in Guadeloupe in the past, still have relic  
563 populations on respectively Dominica and Montserrat islands (Corry *et al.* 2010; Henderson & Powell  
564 2009). Extant *Leiocephalus* mainly inhabit littoral areas, which potentially contributed to the early  
565 demise of the genus in the Lesser Antilles (Breuil 2009), especially as the dry forests typical of these  
566 environments were heavily exploited by humans from the outset of the colonial period (Lugo *et al.*  
567 1981). However, the key to fully understand the history of *Leiocephalus* requires the construction of a  
568 precise regional chronology, unfortunately and although well-documented in Guadeloupe and

569 Martinique, the putative occurrence and extinction dates of *Leiocephalus* on the other Lesser Antillean  
570 islands is far from clear.

571 In Anguilla, *Leiocephalus* is estimated to have gone extinct in the mid-Holocene  
572 (Roughgarden & Pacala 1989) based on data collected from a single site. However, this appears  
573 insufficient to support a mid-Holocene extinction, as the occurrence of a given taxa in a natural or  
574 archaeological deposit can be influenced by several factors (e.g. accumulation agent, changes in local  
575 environmental conditions). The additional mention of *Leiocephalus* on Anguilla (Pregill *et al.* 1994)  
576 remains undated, exposing one of the main issues for the study of fossil *Leiocephalus* in the Lesser  
577 Antilles; the extreme rarity of remains in faunal assemblages from archaeological deposits dating to  
578 the two last millennia. In fact, apart from the Indian Town Trail site in Barbuda (Watters *et al.* 1984)  
579 and several unpublished deposits in Guadeloupe investigated by one of us (Bochaton 2016),  
580 *Leiocephalus* remains have never been reported from archaeological deposits in the Lesser Antilles.

581 The lack of dated fossils and their rarity raises two possibilities; 1) *Leiocephalus* species were  
582 almost entirely extinct more than two thousand years ago and are thus logically absent from Lesser  
583 Antillean archaeological deposits that predate the human colonization of the islands or, 2) their  
584 absence reflects biases in the identification of fossil remains or the composition of faunal assemblages  
585 from open-air archaeological deposits. These issues are not specific to *Leiocephalus*, as recently  
586 demonstrated by the similar complete absence of *Boa* snakes in regional archaeological sites, pattern  
587 which has potentially been linked to specific Amerindian cultural practices (Bochaton 2020). A similar  
588 lack of past occurrence data was also used to support an early Holocene extinction of *Diploglossus* in  
589 the Lesser Antilles (Underwood 1964; although see Bochaton *et al.* 2016 for rare archaeological data  
590 contradicting this position). It is possible that the small size and relative morphological similarity with  
591 other lizard bones renders identifying *Leiocephalus* specimens from archaeological deposits difficult.  
592 In this respect, it is interesting to note that rare archaeological taxa, such as *Leiocephalus* (Bailon *et al.*  
593 2015; Boudadi-Maligne *et al.* 2016; Kemp & Hadly 2016; Pregill *et al.* 1994; Roughgarden & Pacala  
594 1989; Stouvenot *et al.* 2014; Watters *et al.* 1984), *Boa* (Bochaton 2020; Bochaton & Bailon 2018), and  
595 *Diploglossus* (Bochaton *et al.* 2016), were mentioned only by trained paleo-herpetologists. This lack



596 of archaeological data concerning *Leiocephalus* is thus not a good argument for their absence during  
597 the Amerindian and historical periods. These lizards might have disappeared during the second half of  
598 the 19<sup>th</sup> century colonial period, which would explain why they were overlooked by the biologists who  
599 provided the first descriptions of fauna in the West Indies.

#### 600 Past diversity and colonization history of *Leiocephalus* in the Lesser Antilles

601 The geological history of the West-Indies is complex as the geography of this area, especially its  
602 southern part, has undergone massive changes across the last 50 million years. The West-Indies have  
603 been mainly colonized in Late Eocene to early Oligocene times from South America (Blackburn *et al.*  
604 2020; Delsuc *et al.* 2019) thanks to a land bridge linking the Greater Antilles to the continent  
605 (Iturralde-Vinent 2006; Marivaux *et al.* 2020). This landmass however disappeared in the Late  
606 Oligocene while a much younger chain of islands emerged eastward (the modern Lesser Antilles)  
607 (Philippon *et al.* 2020). As an effect of this rich geological history several events can be drawn to  
608 explain the colonization of the Lesser Antillean islands with overwater dispersal events from South  
609 America, the Greater Antilles, or another still visible or nowadays disappeared island. Regarding  
610 *Leiocephalus*, hypotheses of its initial colonization of the Lesser Antilles vary according to the  
611 phylogenetic position of this genus. These lizards were first considered as “Tropiduridae” (Frost &  
612 Etheridge 1989) native to South America, prior to being found to be closer to North American genera  
613 (Hedges 1996). Recent molecular data indicates Leiocephalidae to be either a basal pleurodont  
614 squamate (Pyron *et al.* 2013) or a sister taxon to all pleurodont squamates (Zheng & Wiens 2016),  
615 making it difficult to pinpoint where they first appeared in the West Indies. Leiocephalidae and other  
616 pleurodont squamates diverged 91 My years ago (Zheng & Wiens 2016), which would considerably  
617 predate the K/T crisis and the divergence time of all Antillean taxa (Hedges 2006). Given the current  
618 absence of molecular data for Lesser Antillean *Leiocephalus*, it is difficult to evaluate the reliability of  
619 our morphology-based cladistic analysis. In addition, considering the changing position of  
620 Leiocephalidae since the initial work of Pregill (1992), it is also possible that the character states  
621 identified as “primitive” or “derived” need to be reevaluated in light of the past phylogenetic position of  
622 *Leiocephalus*. This renders interpreting our results concerning the existence of a basal Lesser Antillean

623 clade more complex. Despite these uncertainties, if we accept the phylogenetic proximity between *L.*  
624 *herminieri* and *L. roquetus*, and a basal position in their genus clade, our results would suggest an  
625 initial colonization of the Cenozoic Antilles from South America just as it is the case for most other  
626 terrestrial taxa. However, in the absence of molecular data for each modern species and fossil data  
627 predating the Late Pleistocene for most of the West Indies, it is currently impossible to integrate this  
628 potential scenario within what is likely to be very old and complex colonization that included multiple  
629 extinction events. The history of *Leiocephalus* in the West Indies is probably significantly more  
630 complex than the majority of modern taxa, rodents for example (Marivaux *et al.* 2020) which  
631 colonized the region following either the formation of the Aves Ridge during the Oligocene or who  
632 dispersed after the emergence of the modern islands (Hedges 2006).

### 633 **Conclusion**

634 Our results highlight the interest of revisiting old museum and private collections that, at first glance,  
635 appear to hold no genuine scientific interest. The discovery of a dry specimen of an extinct taxon only  
636 previously documented by fossil remains allowed us to describe an endemic extinct species, provide  
637 additional details about the timing of its extinction, and advance a hypothesis concerning the past  
638 radiation of the genus *Leiocephalus* in the Lesser Antilles. This exceptional discovery is likely due to  
639 the important circulation of “exotic” goods from the Caribbean between the 17<sup>th</sup> and 19<sup>th</sup> centuries and  
640 suggests that other interesting natural history specimens have ended up in private collections and then  
641 in regional museums the world over. Like the example described here, these specimens are often of  
642 uncertain origin and history. However, as we have shown, comparisons with fossil data of well-  
643 documented origin can overcome these issues. The combination of fossil and modern data provide a  
644 robust comparative framework for future studies of Caribbean *Leiocephalus* and reveals a wide  
645 diversity of extinct lizards that likely remains to be described in the Lesser Antilles.

646

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657

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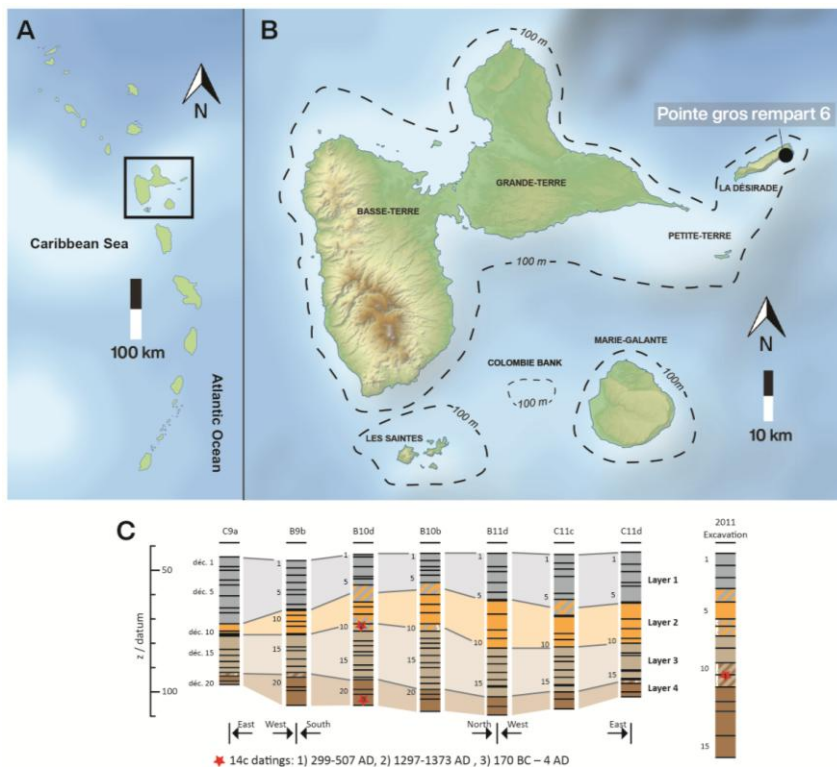
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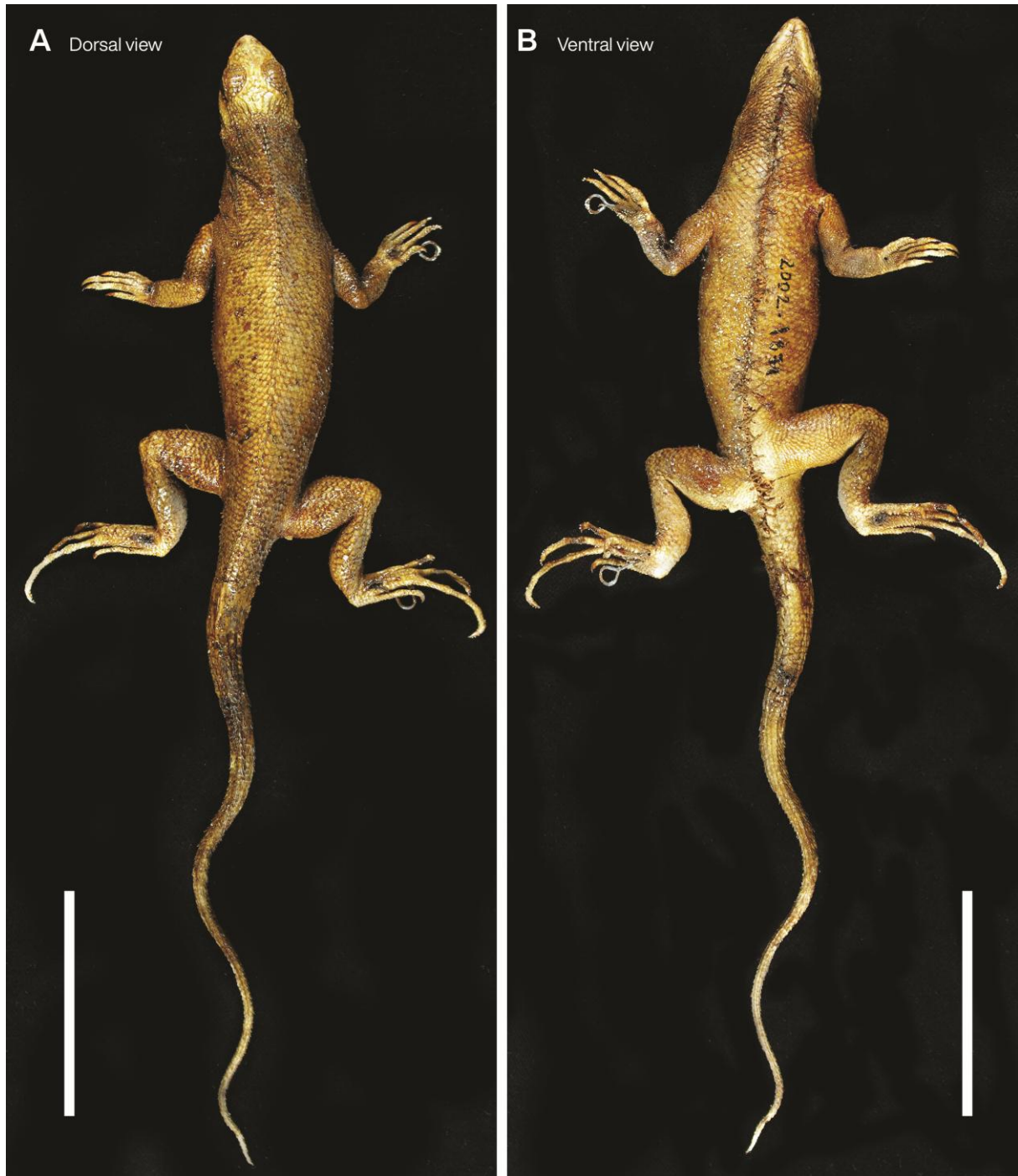
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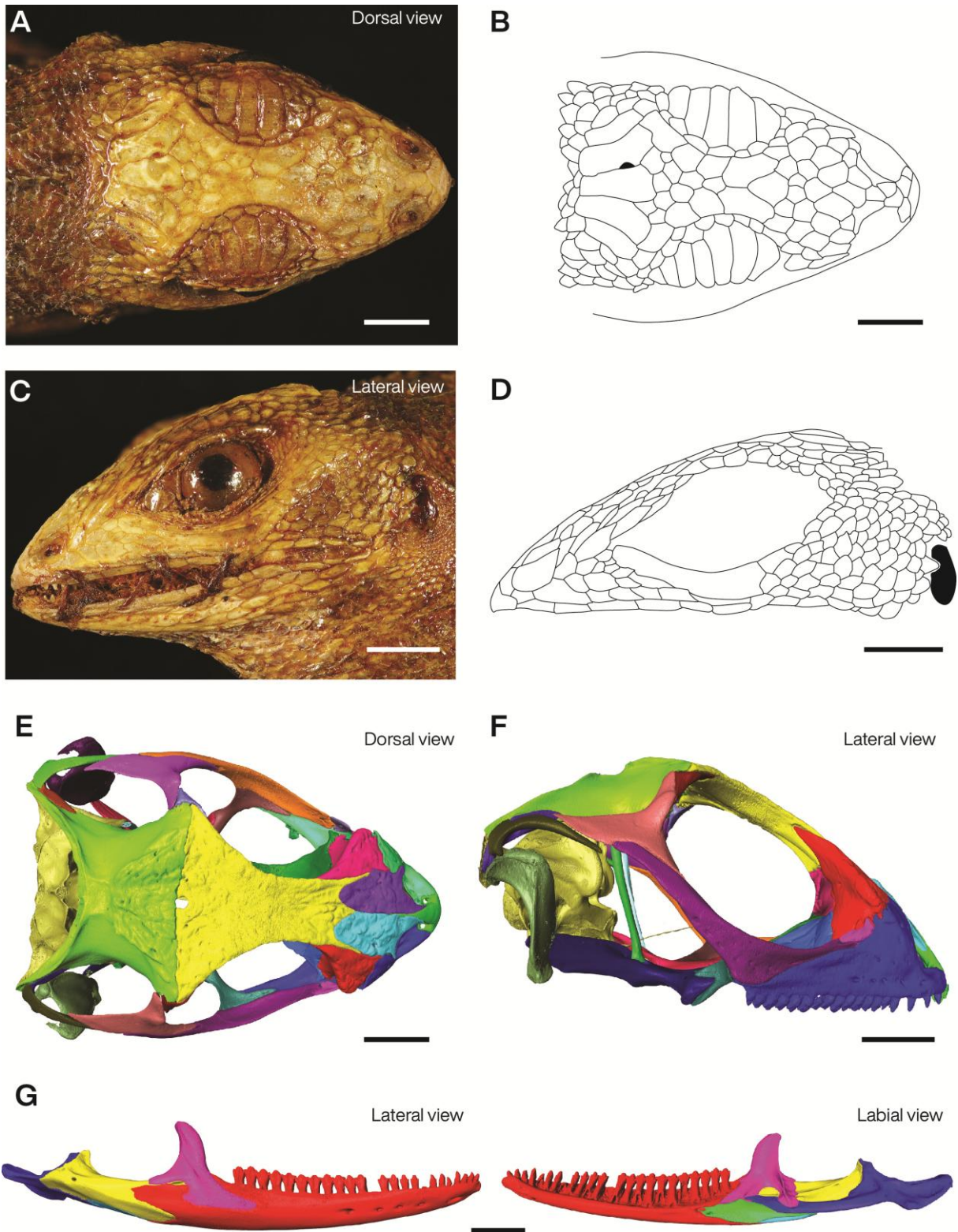


855 Figure 1: A) Map of the Lesser Antilles with the location of the Guadeloupe islands; B) Map of the  
856 Guadeloupe islands with the location of the PGR6 deposit and indication of the -100 meters marine  
857 isobath; C) Stratigraphic correspondence between the squares and *décapages* of the 2016 PGR6  
858 excavation and those of the 2011 excavation with locations of the three 14c dates performed.



859

860 Figure 2: Dorsal (A) and ventral (B) views of the complete holotype specimen of *Leiocephalus*  
861 *roquetus* sp. nov. (MHNBx 2002.1871). Scale bar= 5 mm.



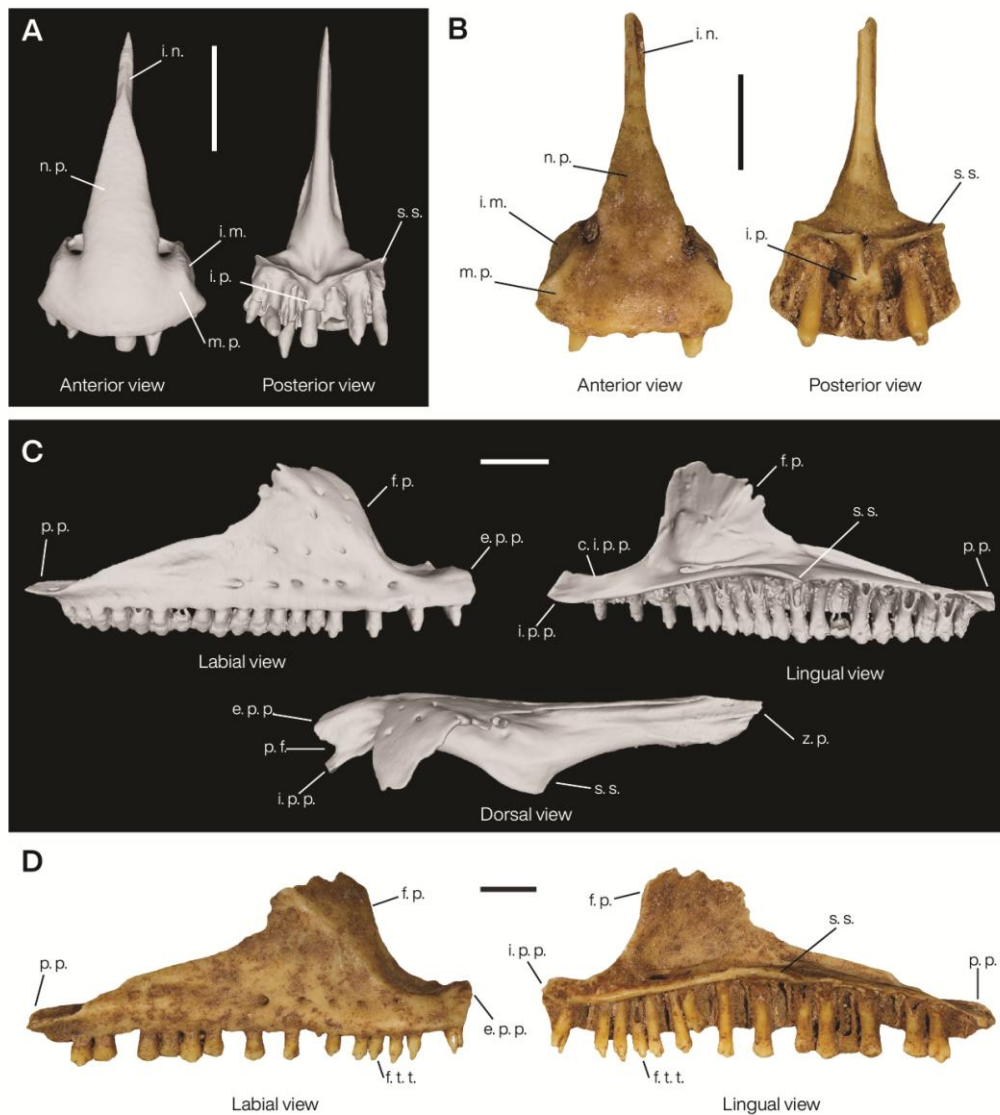
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863 Figure 3: Head and skull of the Holotype of *Leiocephalus roquetus* sp. nov. (MHNbX 2002.1871). A,

864 B: Picture and drawing of the dorsal scales of the head of the Holotype; C, D: Picture and drawing of

865 the lateral scales of the head of the Holotype; E, F: Dorsal and lateral views of the 3D model of the

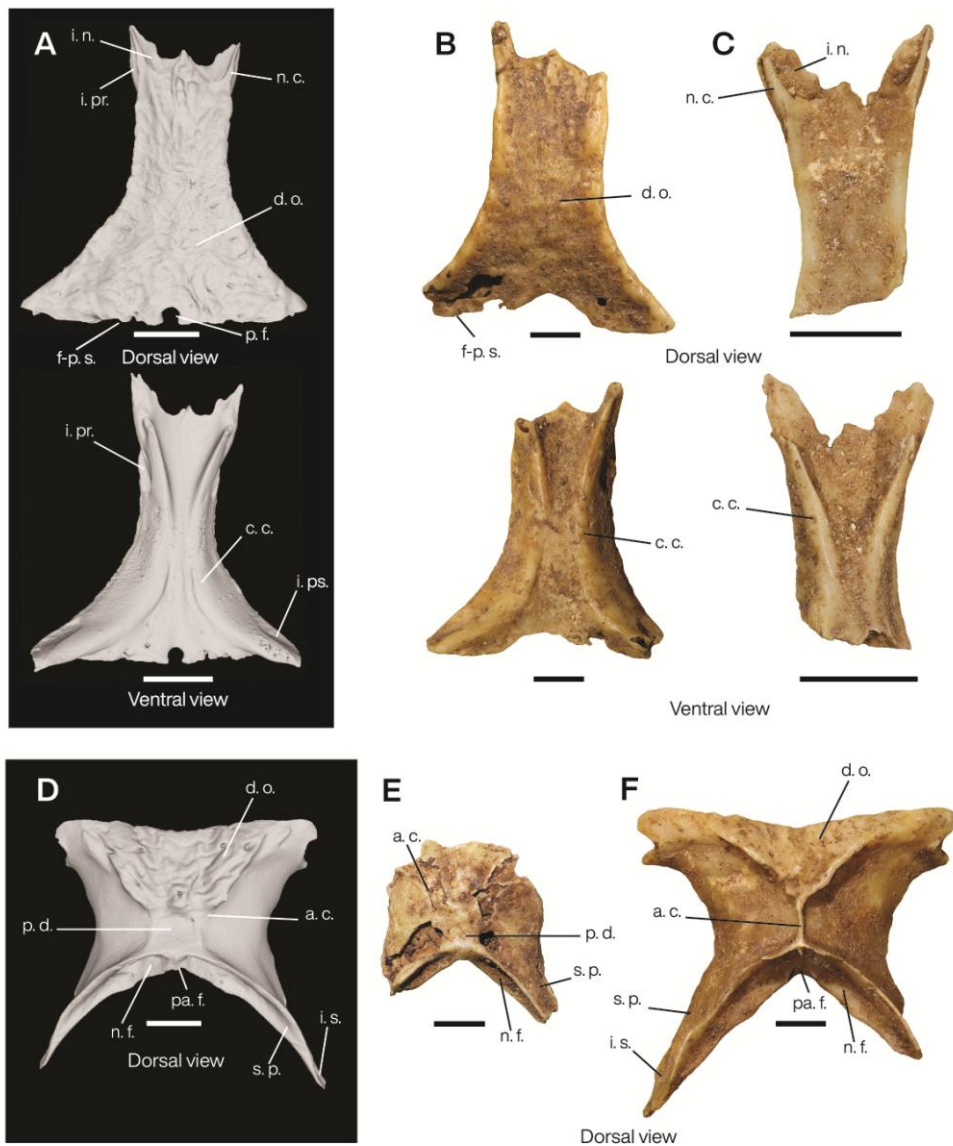
866 skull of the holotype; G: Labial and lingual views of the 3D model of the right mandible of the  
 867 holotype. Scale bars= 3 mm.



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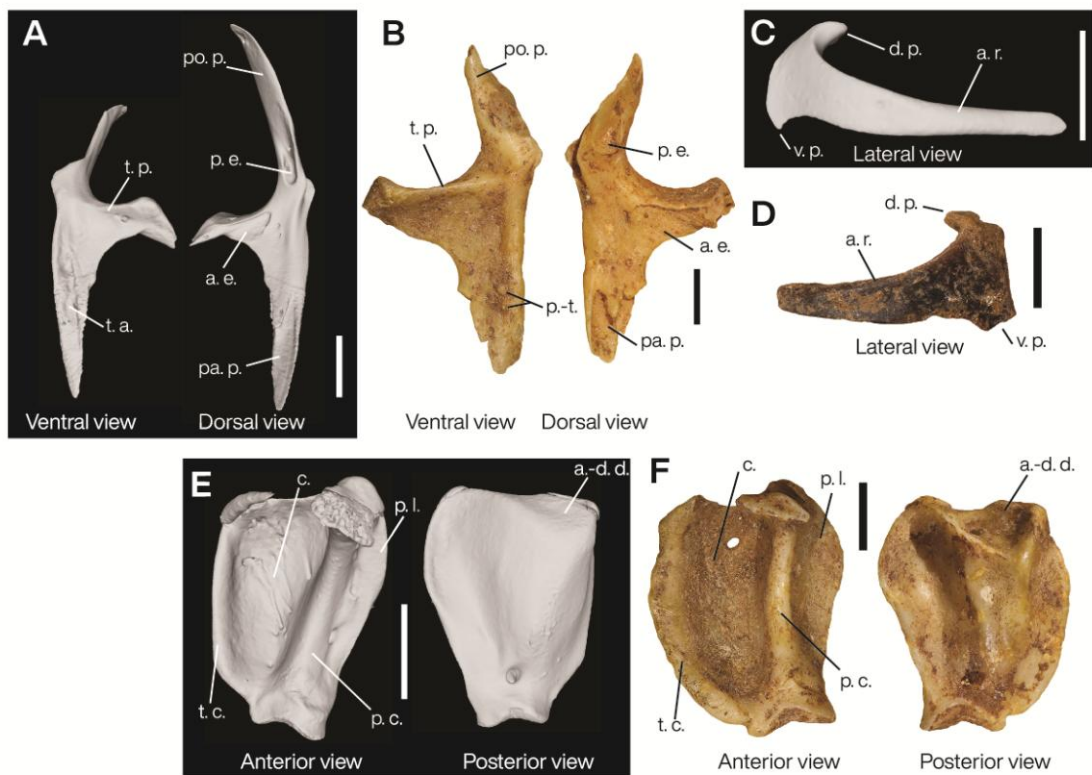
869 Figure 4: Premaxilla and maxilla of *Leiocephalus roquetus* sp. nov. A: 3D Model of the premaxilla of  
 870 the holotype (MHNbX 2002.1871); B: Paratype “PGR6. square C11c. *décapage* 14.XII” collected in  
 871 PGR6 deposit. C: 3D Model of the right maxilla of the holotype (MHNbX 2002.1871); D: Paratype  
 872 “PGR6. square B10d. *décapage* 22.III” (right) collected in PGR6 deposit. Abbreviations: **c. i. p. p.**:  
 873 crest of the internal premaxillary process, **e. p. p.**: external premaxillary process, **f. p.**: facial process, **f.**

874 **t. t.:** first most anterior tricuspid tooth, **i. m.:** imprint of the maxilla, **i. n.:** imprint of the nasal bone, **i.**  
 875 **p.:** incisive process, **i. p. p.:** internal premaxillary process, **m. p.:** maxillary process, **n. p.:** nasal  
 876 process, **p. f.:** premaxillary fenestra, **s. s.:** supradental shelf, **z. p.:** zygomatic process. Scale bars=  
 877 2mm.



878  
 879 Figure 5: Frontal and parietal bones of *Leiocephalus roquetus* sp. nov. A: 3D Model of the frontal  
 880 bone of the holotype (MHNbx 2002.1871); B: Paratype frontal bone “PGR6. square B10d. *décapage*  
 881 13.IV” collected in PGR6 deposit; C: Paratype frontal bone “PGR6. square B10d. *décapage* 13.V”

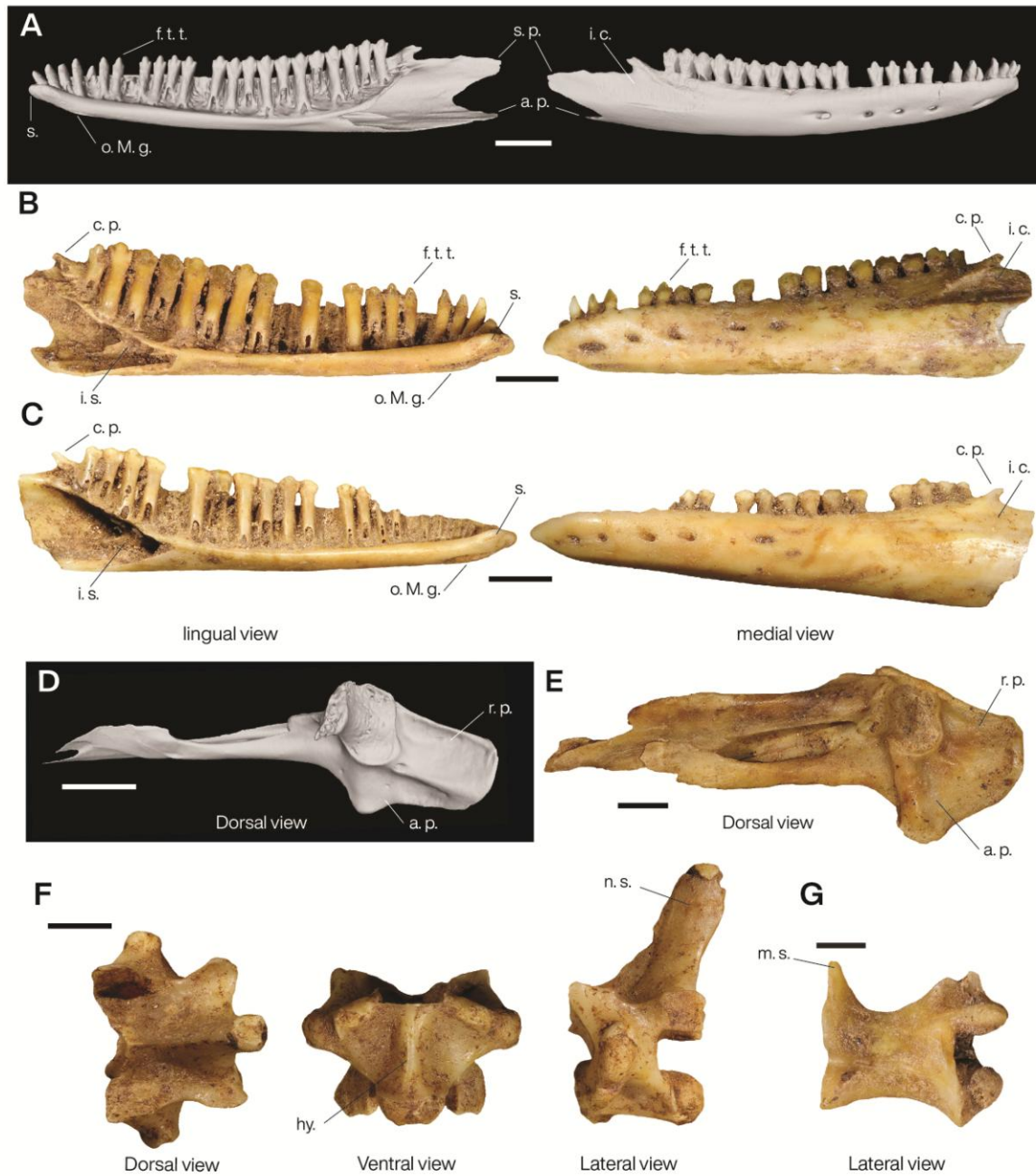
882 collected in PGR6 deposit; D: 3D Model of the parietal bone of the holotype (MHNBx 2002.1871); E:  
 883 Paratype parietal bone “PGR6. square C11d. *décapage* 12.VI” collected in PGR6 deposit; F: Paratype  
 884 parietal bone “PGR6. square B9b. *décapage* 22.VII” collected in PGR6 deposit. Abbreviations: **a. c.:**  
 885 adductor crest, **c. c.:** cranial crest, **d. o.:** dermal ornamentation, **f-p. s.:** fronto-parietal suture, **i. n.:**  
 886 imprint of the nasal bone, **i. pr.:** imprint of the prefrontal bone, **i. ps.:** imprint of the postfrontal bone,  
 887 **i. s.:** imprint of the supratemporal bone, **n. c.:** nasal process crest, **n. f.:** nuchal fossa, **pa. f.:** parietal  
 888 fossa, **p. d.:** postero-medial depression, **p. f.:** parietal foramen, **s. p.:** supratemporal process. Scale  
 889 bars= 2mm.



890

891 Figure 6: Pterygoid, squamosal and quadrate bones of *Leiocephalus roquetus* sp. nov. A: 3D Model of  
 892 the right pterygoid of the holotype (MHNBx 2002.1871); B: Paratype left pterygoid bone “PGR6.  
 893 square C11d. *décapage* 14.X” collected PGR6 deposit; C: 3D Model of the right squamosal of the  
 894 holotype (MHNBx 2002.1871); D: Paratype left squamosal bone “PGR6. square B9b. *décapage*

895 22.IX” collected in PGR6 deposit; E: 3D Model of the left quadrate of the holotype (MHNbx  
896 2002.1871); F: Paratype left quadrate bone “PGR6. square C11c. *décapage* 15.XI” collected in PGR6  
897 deposit. Abbreviations: **a.-d. d.**: antero dorsal depression, **a. e.**: articular surface with the ectopterygoid  
898 bone, **a. p.**: articular surface with the palatine bone, **a. r.**: anterior ramus, **c.**: conch, **d. p.**: dorsal  
899 process, **p. c.**: posterior crest, **p. e.**: pit for the insertion of the epipterygoid, **p. l.**: pterygoid lamina, **p.**  
900 **t.**: pterygoid teeth?, **pa. p.**: palatine process, **po. p.**: posterior process, **t. c.**: tympanic crest, **t. p.**:  
901 transverse process, **t. s.**: tooth socket, **v. p.**: ventral process. Scale bars= 2mm.

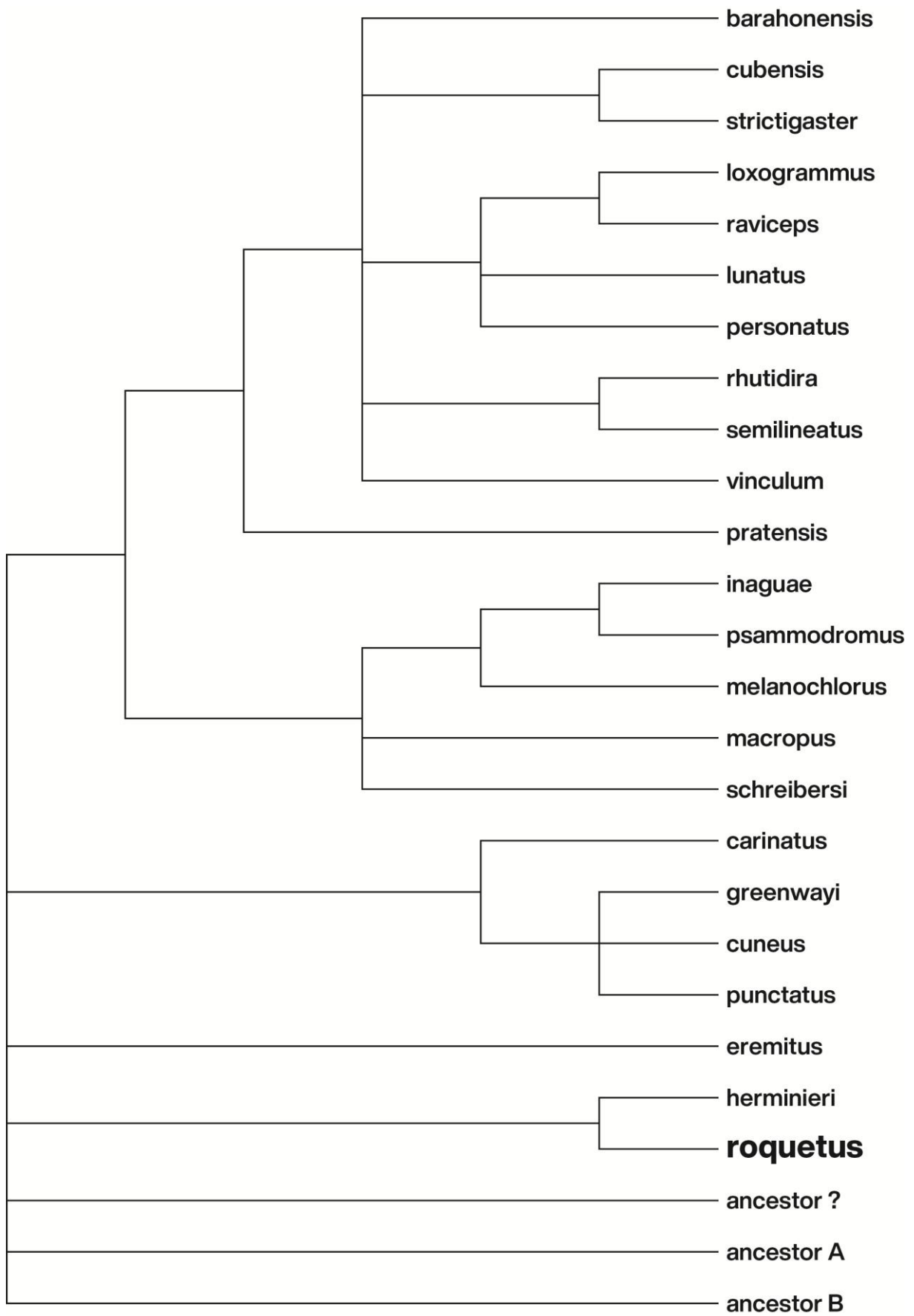


902

903 Figure 7: Dentary, articular bones and vertebrae of *Leiocephalus roquetus* sp. nov. A: 3D Model of the  
 904 right dentary of the holotype (MHNbx 2002.1871); B: Paratype dentary “PGR6. square C11d.  
 905 *décapage* 16.I” (left) collected in PGR6 deposit; C: Paratype dentary “PGR6. square C11c. *décapage*  
 906 11.II” (left) collected in PGR6 deposit; D: 3D Model of the right articular of the holotype (MHNbx  
 907 2002.1871); E: Paratype articular “PGR6. square B9b. *décapage* 17.VIII” (right) collected in PGR6

908 deposit; F: Anterior trunk vertebra collected in the layer 4 of PGR6 (square B10d, *décapage* 20); G:  
909 Caudal vertebra collected in the layer 2/3 of PGR6 (square B10d, *décapage* 10). Abbreviations: **a. p.**:  
910 angular process, **c. p.**: coronoid process, **f. t. t.**: first most anterior tricuspid tooth, **hy.**: hypapophysis, **i.**  
911 **c.**: lateral imprint of the coronoid bone, **i. s.**: intra-mandibular septum, **m. s.**: medial spine, **n. s.**: neural  
912 spine, **o. M. g.**: anterior opening of the Meckelian groove, **r. p.**: retroarticular process, **s.**: symphysis,  
913 **sy.**: synapophysis, **s. p.**: surangular process. Scale bars=2 mm.





915 Figure 8: Consensus phylogenetic tree of modern and fossil Lesser Antillean species of *Leiocephalus*  
916 showing the strong proximity between *L. roquetus* sp. nov. and *L. herminieri*. This tree was obtained  
917 from the 177 most parsimonious trees (130 steps). In this tree, “ancestor ?” is the theoretical ancestor  
918 used by Pregill (1992). The two other theoretical ancestors “ancestor A” and “ancestor B” are similar  
919 to “ancestor ?” but for these “taxa” the characters recorded as “?” in the “ancestor” of Pregill (1992)  
920 have been respectively replaced by “0” and “1” character states.

921

922 Appendix 1. Character matrix used in the phylogenetic analysis

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924