



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

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### Abstract

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

**Key words:** Curlytail lizard, Extinction, Human Impact, Lesser Antilles, Osteology

### Introduction

The West Indies are known to have been severely impacted over the last several hundred to thousand years by both climatic and anthropogenic events that reshaped most of their biological diversity. The rich historical, archaeological, and paleontological records of these islands reveal hundreds of extinction events touching all taxa and regions (Cooke *et al.* 2017; Orihuela *et al.* 2020; Steadman *et al.* 2015). The causes underlying these extinctions have been the subject of considerable debate, as early research focused almost uniquely on the Pleistocene–Holocene transition as the main extinction factor (e. g. Pregill & Olson 1981; Underwood 1964). However, numerous recent work has demonstrated the considerable impact of human colonization and anthropization that led to the extinction of a relatively substantial portion of the local biodiversity (Bochaton *et al.* 2015b; Cooke *et al.* 2017; Soto-Centeno & Steadman 2015; Steadman *et al.* 1984, 2015). These studies also demonstrated the West Indies to be a perfect case study for exploring the long term impact of humans on island ecosystems in the framework of the current mass extinction crisis (Barnosky *et al.* 2011; Ceballos *et al.* 2015, 2017). Of the taxa impacted by these extinction events, several were almost completely wiped out from the Lesser Antilles. This group of strongly affected taxa comprises multiple squamates, including diploglossine lizards (Bochaton *et al.* 2015a, 2016), *Boa* snakes (Bochaton 2020; Bochaton & Bailon 2018) and leiocephalid lizards (Etheridge 1964; Pregill *et al.* 1988) the latter, which despite being one of the few squamate genera endemic to the West Indies, still remains poorly understood. The monophyly of the *Leiocephalus* (Gray 1827) species restricted to the West Indies was documented in the 1960s (Etheridge 1966) and confirmed by molecular evidence (Pyron *et al.* 2013), with the members of this genus first included in their own subfamily and then family (Leiocephalidae Frost & Etheridge 1989). The genus *Leiocephalus* currently comprises 24 species exclusively distributed in the Greater Antilles (Hedges 2020), including seven extinct species,

five of which are known only from fossil remains (Pregill 1992). Among these extinct species, two were endemic to the Lesser Antilles, an area where no *Leiocephalus* species are currently known. The first of these species is *Leiocephalus herminieri* (Duméril & Bibron 1837), whose fluid-preserved type specimens were collected in Martinique during the 19<sup>th</sup> century (for a discussion concerning the origin of these specimens see Breuil -2002-). The second species is *Leiocephalus cuneus* Etheridge, 1964, a taxa that was originally described on the basis of fossil remains collected in Barbuda (Etheridge 1964; Watters *et al.* 1984) but whose distribution was later extended to Antigua (Pregill *et al.* 1988), and possibly to Anguilla, La Désirade, and Marie-Galante (Bailon *et al.* 2015; Boudadi-Maligne *et al.* 2016; Pregill 1992; Pregill *et al.* 1994; Stouvenot *et al.* 2014). The distribution of this taxon outside Barbuda and Antigua is however doubtful, as no clear fossil evidence is currently available. In Guadeloupe, the past occurrence of *Leiocephalus* lizards was mentioned in several historical texts (Breuil 2002; Du Tertre 1654; de Rochefort 1658) although their precise taxonomic identification is unclear. Historical data and biogeographic hypotheses all suggest that *Leiocephalus* may have previously been widespread in the Lesser Antilles. The current fossil record may therefore be substantially unrepresentative of the past diversity of this lizard. The phylogenetic relationships between both modern and fossil *Leiocephalus* species are also poorly understood. Until recently, the most comprehensive study of this genus concerned morphological characters combining both modern and known fossil taxa (Pregill 1992). However, none of the clades recognized in this pioneering work were confirmed by the few non-exhaustive molecular analysis conducted since (Köhler *et al.* 2016; Pyron *et al.* 2013). In addition, both morphological and molecular analyses seem to indicate a complex colonization scenario comprising multiple colonization events. Overall, the history and past diversity of the genus *Leiocephalus* in the Lesser Antilles is poorly documented. For example, we currently do not know how these species were diversified in this area, where they came from, and when and why they went extinct. Here we provide important new descriptions of both historical and fossil specimens of *Leiocephalus* collected in Guadeloupe that we attribute to a new endemic species: *Leiocephalus roquetus* **sp. nov.**

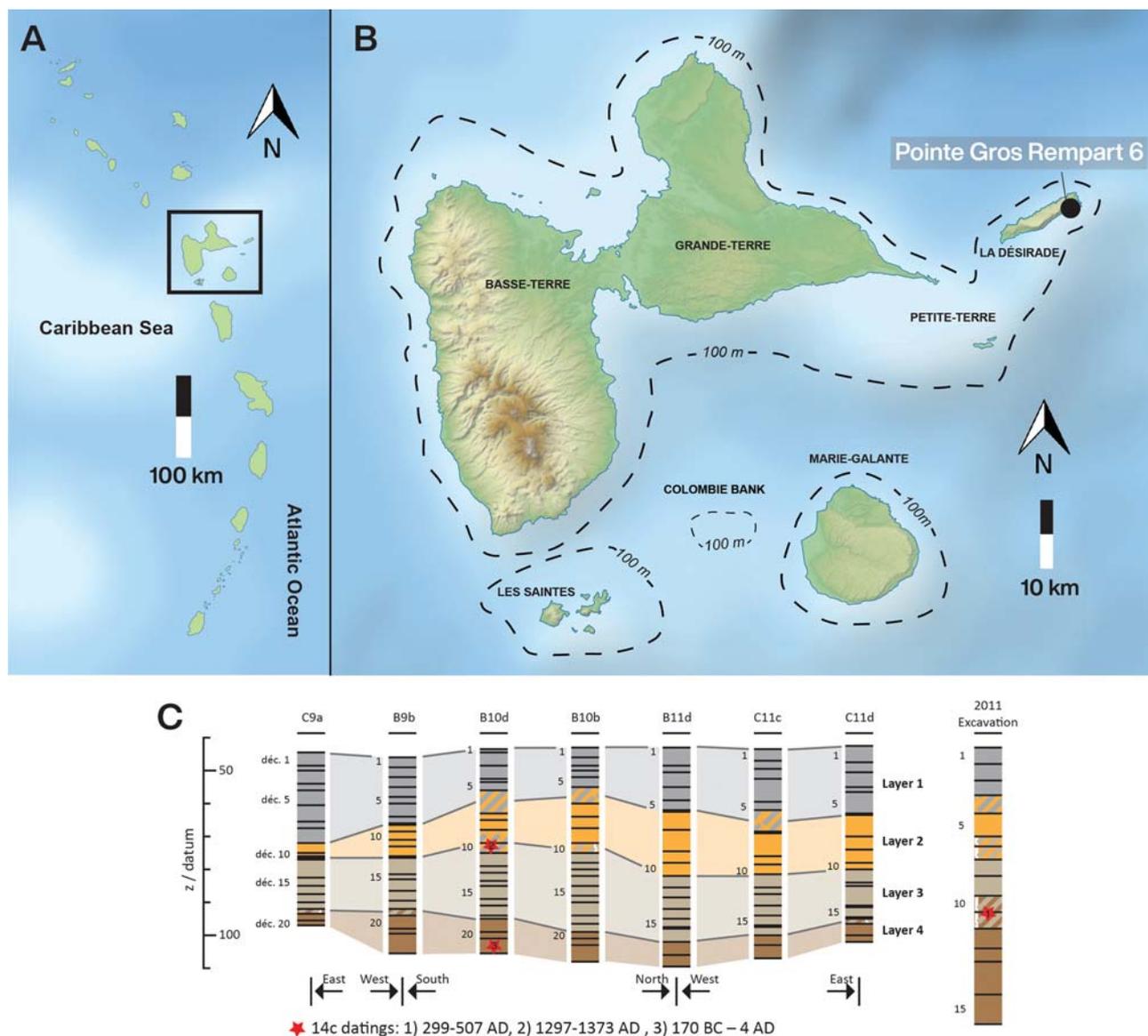
## Materials and method

**Dry museum specimen.** The holotype of *Leiocephalus roquetus* **sp. nov.** is a dry taxidermy specimen stored in the Natural History Museum of Bordeaux (MHNbx) in France. The specimen was donated to the museum around 1835 by Théodore Roger (1784–1838), an alcohol manufacturer and naturalist better known for his collection of Lepidoptera. Very few details are available concerning the origin of the holotype specimen; it is stored with a label reading “Holotropide de l’Herminier *Holotropis herminieri* Gray Guadeloupe donation Roger” with the species author’s name “*herminieri*” erroneously attributed to Gray, and “Guadeloupe” being the geographic origin of the specimen. This label is, in fact, a mid 20<sup>th</sup> century copy of the original 19<sup>th</sup> century label, and it is possible that some information originally attached to the specimen has been lost. The first catalog record to unambiguously mention this specimen under the name *Holotropis herminieri* Duméril & Bibron, 1837 comes from the beginning of the 20<sup>th</sup> century, suggesting that this specimen remained unidentified for years. The fact that the locality “Guadeloupe” contradicts the (erroneous) species identification (*Leiocephalus herminieri* being endemic to Martinique) is a clue that the origin was originally already attached to the specimen as it was not inferred from what is potentially a more recent taxonomic attribution. Although the general interest of this specimen was previously recognized (Breuil 2009), it remained unstudied until now.

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

*Regional de l'Archéologie de Guadeloupe*, we plan to petition for these bones described as paratypes to be united with the holotype dry-specimen in a single collection housed at the Natural History Museum of Bordeaux.

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



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

The 2016 excavations helped clarify the chronology of the four stratigraphic units identified during the initial work at the site (Fig. 1–B). An initial radiocarbon date obtained on a sample recovered during the 2011 excavations provided an age of 299-507 cal. AD for the base of the layer 3. Two additional radiocarbon dates, one on charcoal

(Lyon-14287 –SacA-50616-) recovered from the base of layer 4 (square B10d, *décapage* 22) provided a date of 170 BC—4 cal. AD (2060±30 BP), the other on a Yellow-crowned night-heron bone (Lyon-14478 -SacA-51014-) from the top of the layer 3 (square B10d, *décapage* 11) produced a date of 1297-1373 cal. AD (600 ± 30 BP). These new dates are in good agreement with the initial chronological interpretation of the stratigraphy based on the archaeological material (pottery sherds and bones of introduced species). Layer 1 has been attributed to modern activity over the last 200 years, layer 2 to the Colonial period, and layers 3 and 4 to the pre-Columbian Ceramic period between around 200 BC and 1728 AD. The pre-Columbian Ceramic era is divided into different sub-periods spanning from 80 AD to around 1600 AD in Guadeloupe (Fitzpatrick 2015; Hofman *et al.* 1999; Keegan *et al.* 2013) and to 1728 AD in La Désirade (Boudadi-Maligne *et al.* 2016). The few ceramic remains recovered from PGR6 do not provide any additional chronological resolution ( for details see Boudadi-Maligne *et al.* 2016).

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

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

**Anatomical descriptions.** The description of the external anatomy of the Holotype follows the same terminology as Pregill (1992). The osteological description mostly follow the nomenclature Fejérvary-Langh (1923) and Evans (2008). This terminology was complemented by other references (Bailon 1991; Klembara *et al.* 2010; Oelrich 1956; Smith *et al.* 2018), some of which are mentioned in the text when needed.

## Results

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

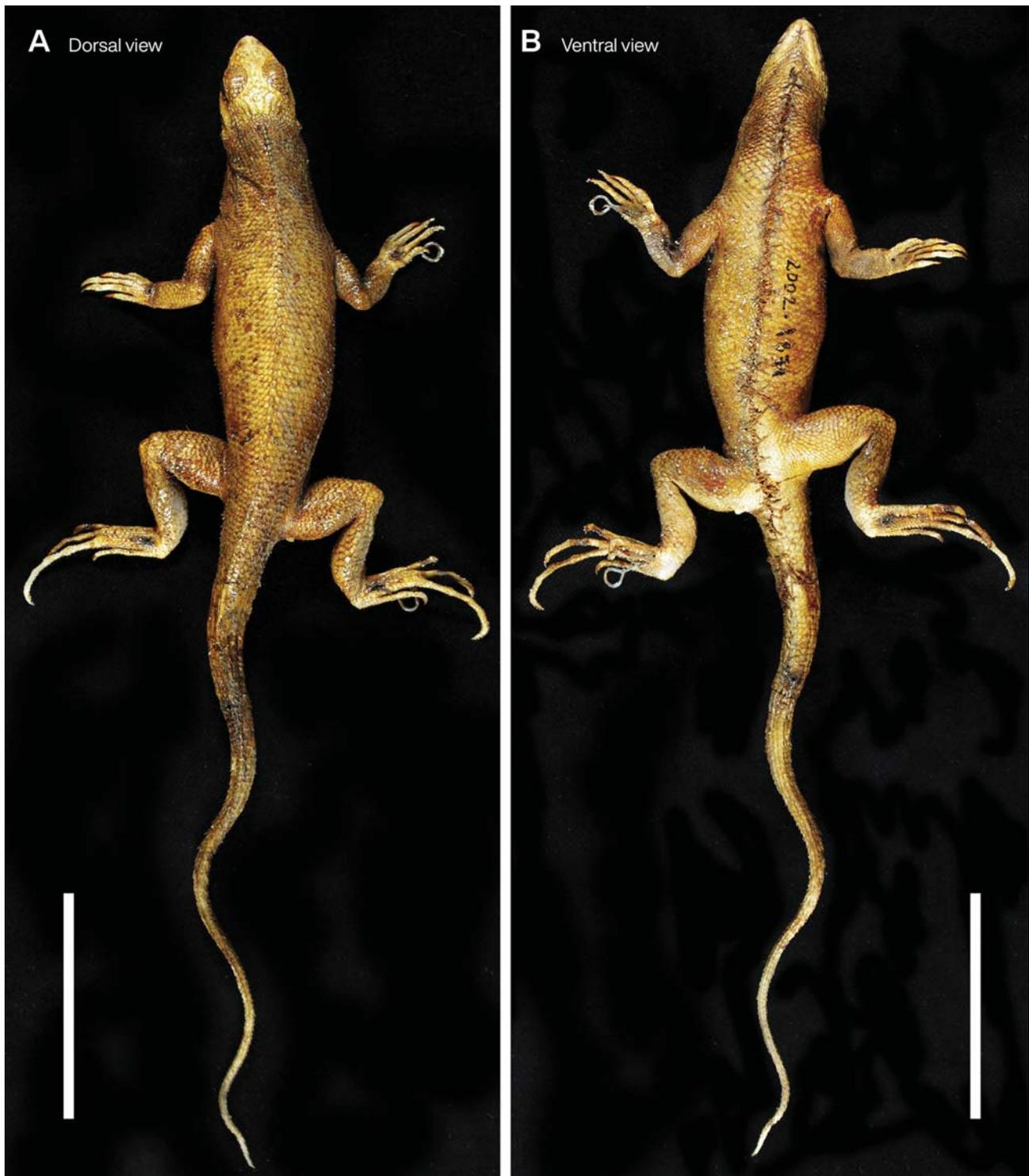
### *Leiocephalus roquetus* **sp. nov.**

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

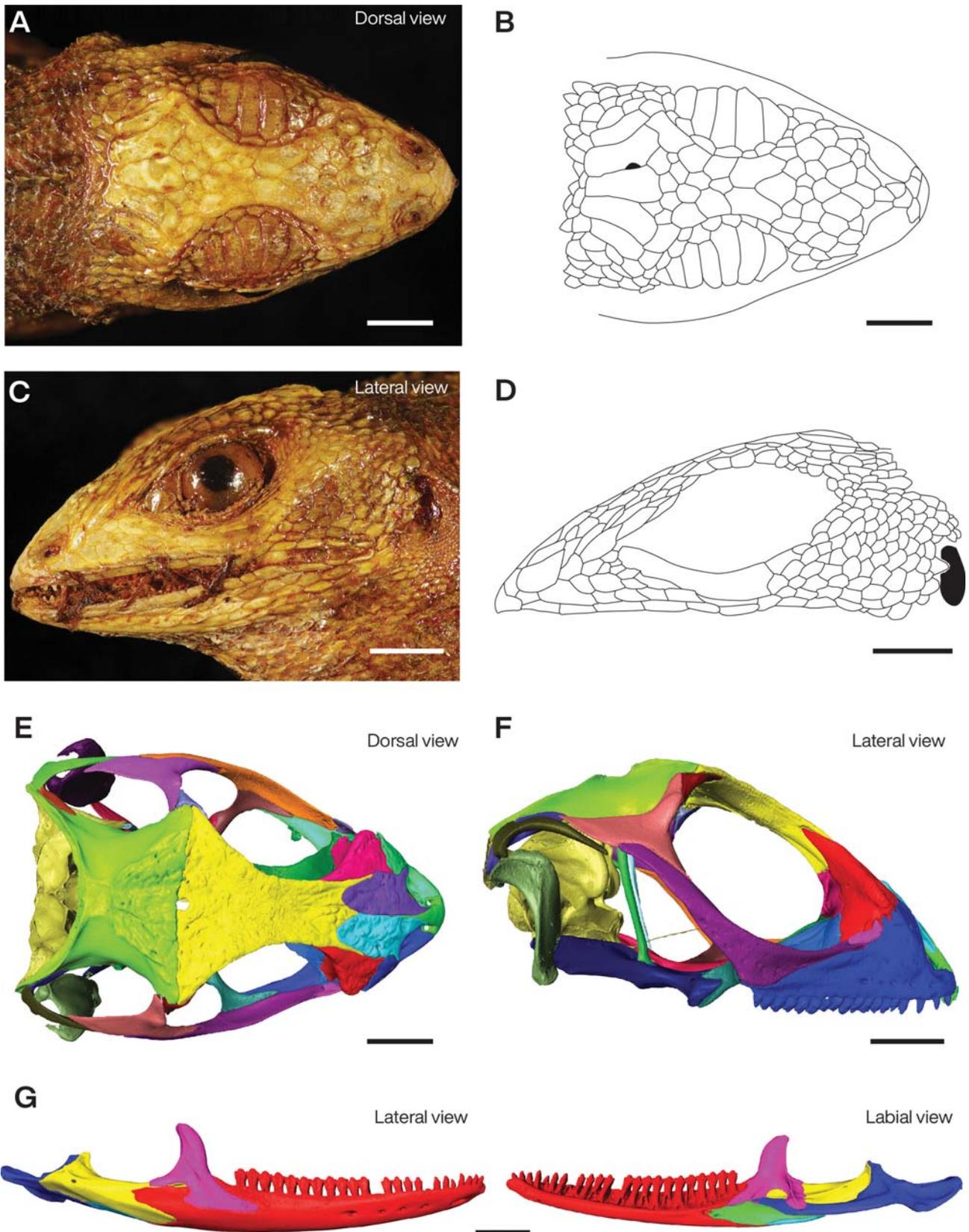
**Diagnosis.** *Leiocephalus roquetus* differs from all other congeners by the morphology of its parietal bone that bears adductor crests fused into a single crest in the posterior area of the bone in large specimens. In addition of this character, *L. roquetus* presents a unique combination of characters: absence of enlarged snout scales, and occurrence of five scales in contact with the first pair of enlarged frontal scales (pattern of type I of Pregill (1992)), the occurrence of three internasal scales, a prominent dorsal body crest, absence of keeled ventral scales, frontal bone exposed dorsally between the nasal and prefrontal bones, skull rugosities on the frontal bone, premaxillary spine constricted just above the dentigerous process, a well-developed posterior process of the septomaxilla, a distinct dorsal process of

the squamosal, a well-developed angular process of the dentary, and transition from bicuspid to tricuspid teeth occurs between the height and sixth most anterior dental position of the dentary. This new taxon also presents several differences with other known Lesser Antillean *Leiocephalus* specimens (see below).

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



**FIGURE 2.** Dorsal (A) and ventral (B) views of the complete holotype specimen of *Leiocephalus roquetus* sp. nov. (MHNbX 2002.1871). Scale bar= 5 mm.



**FIGURE 3.** Head and skull of the Holotype of *Leiocephalus roquetus* sp. nov. (MHNbx 2002.1871). A, B: Picture and drawing of the dorsal scales of the head of the Holotype; C, D: Picture and drawing of the lateral scales of the head of the Holotype; E, F: Dorsal and lateral views of the 3D model of the skull of the holotype; G: Labial and lingual views of the 3D model of the right mandible of the holotype. Scale bars= 3 mm.

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

**General description of the holotype.** The holotype is a complete, dry taxidermy specimen (labeled MHNbx 2002.1871) preserved in the Natural History Museum of Bordeaux (France). This specimen has a snout-vent length (SVL) of 10.8 cm and measures 26.5 cm in total length (Fig. 2). Microtomography reveals the skull to be fully preserved (Fig. 3). The key morphological features of the holotype are as follows: enlarged nasal bones, the narrow nasal process of the premaxilla is triangular, the dorsal part of the premaxilla is fully enclosed by the nasal bones, the premaxilla lacks lateral spines and bears 7 tooth positions, the nasal-maxillary suture is arched toward the mid-line of the snout, the nasal process of the frontal bone is dorsally exposed between the nasal and prefrontal bones, the pterygoid bears teeth but palatine teeth are absent, lacrimal and postfrontal bones are present, the septomaxilla bears a quadrangular lateral wing with a thin posteriorly oriented process, the frontal is narrow with dermal ornamentation, the parietal foramen is on the fronto-parietal suture, the adductor crests of the parietal table converge but do not touch and are posteriorly separated by a depressed area, the anterior part of the parietal table presents a dermal ornamentation, the supratemporal bone is on the lateral side of the supratemporal process of the parietal, the supratemporal process of the squamosal is distinct, splenial and angular bones are present, the angular process of the dentary is well-developed, most of the teeth are tricuspid and distinctively flared, the transition from monocuspid/bicuspid to tricuspid teeth occurs at the seventh dental position on the dentary and at the fourth dental position on the maxilla. Head scales are large, the specimen presents four rows of snout scales of sub-equal size between the internasal and the anterior pair of frontal scales, there are four moderately-sized parietal scales and the most lateral scales are smaller than the median scales, two rows of post parietal scales are present, there is no enlarged lateral post-parietal scale, there are three internasal scales, there are four lorilabial scales anterior to the first lorilabial contacting the elongated sub-ocular scale, the cephalic scales lack ridges, the temporal scales are of sub-equal size and no elongated temporal scales are present, the lateral nuchal scales are smaller than surrounding body scales, the lateral body scales are the same size as dorsal and ventral scales, a prominent middorsal body crest formed by overlapping scales is present, the dorsal crest (occiput to vent) is composed of 53 scales, the tricarnate scales at the base of the first and second toes grow into comb-like fringes but are not prominent, the venter is dull and patternless, there is no scapular patch, no suprascapular blotches, no facial band, and the base of tail is laterally compressed.

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

### **Premaxilla**

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

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

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

### **Maxilla**

**Holotype** (MHNbx 2002.1871) (Fig. 4–C): The bone bears a 12 mm long dental row bearing 21 tooth positions. The most anterior tooth is conical, the second and third are bicuspids with a large posterior cusp and a reduced

anterior cusp. The following teeth are tricuspid (with a dominant central cusp), linguolabially compressed, distinctively flared in mesio-distal direction. The shape of these teeth is similar to that of tricuspid teeth of the dentary (see below). In medial view, the supradental shelf (*sensu* Rage & Augé 2010) is slightly arched toward the mid-length of the bone. The facial process is triangular, longer than it is high. The posterior process is short, and is in equivalent in length to the portion of the supradental shelf bearing the two last dental positions, and its posterior tip is quadrangular in dorsal view. In labial view, the antero-dorsal margin of the facial process is strongly inflected medially. The surface of the facial process is punctuated by several small foramina, and six larger labial foramina are present. The bone lacks dermal ornamentation. In dorsal view, the supradental shelf is triangular. The internal premaxillary process is more developed than the external one. This process is high and thin, and its antero-dorsal margin is linked to the medial margin of the facial process by a crest visible in medial view. A moderately deep V-shaped premaxillary fenestra separates the internal and external premaxillary processes.

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

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

### **Frontal bone**

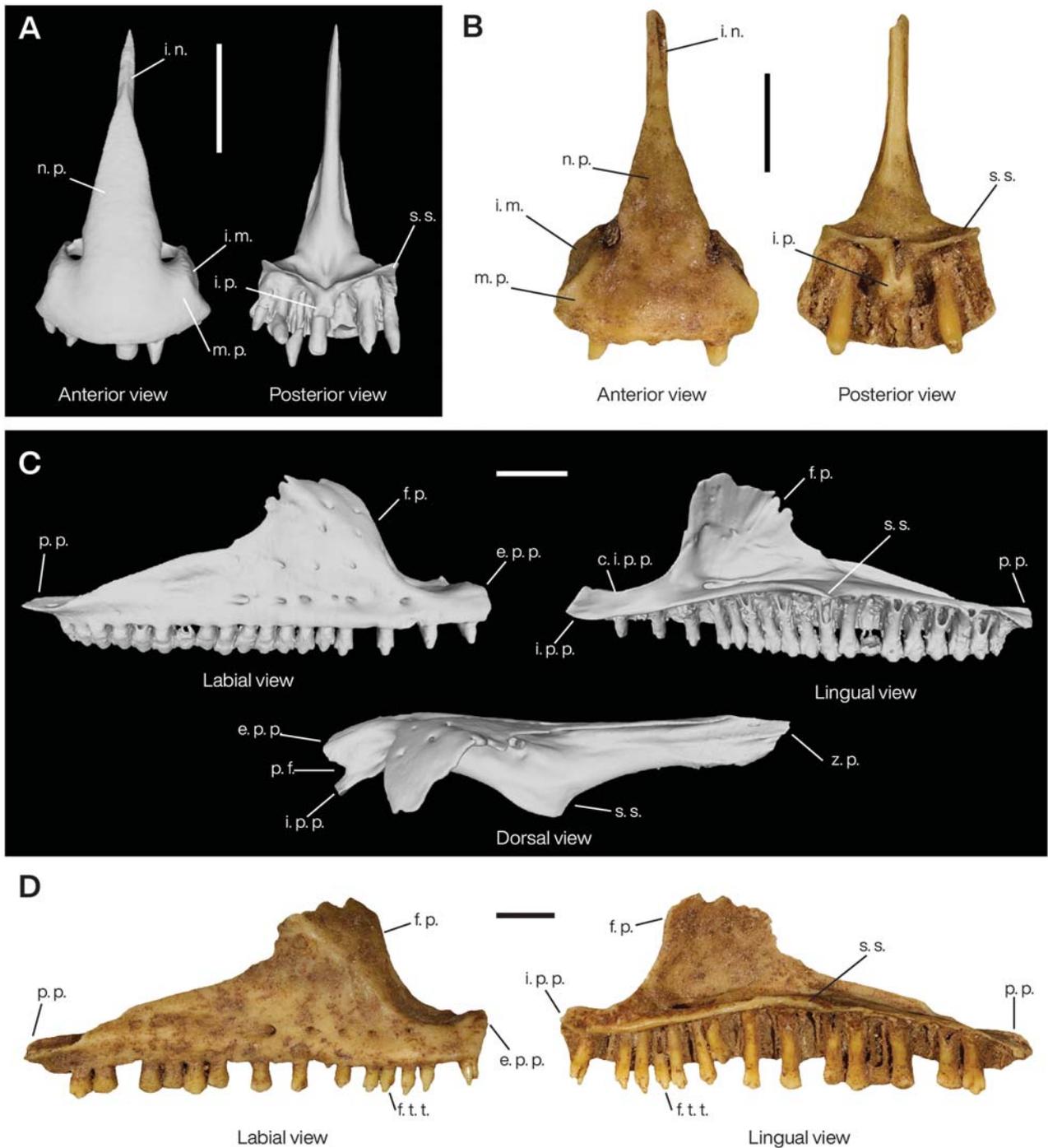
**Holotype** (MHNbx 2002.1871) (Fig. 5–A): The two frontal bones are fused (azygous). In dorsal view, the bone is elongated, 2.5 times wider in its posterior than in its anterior part, with a nearly straight parietal margin. The minimal width of this element at the level of its median constriction is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

**Paratypes** “PGR6. square B10d. *décapage* 13.IV” (Fig. 5–B), and “PGR6. square B10d. *décapage* 13.V” (Fig. 5–C): These bones were both found in layer 3 of PGR6 (square B10d, *décapage* 13) and correspond to a large individual with a minimal width of 4.9 mm and a small specimen, probably a juvenile, with a minimal width of 2.2 mm. These specimens are morphological similar to the holotype.

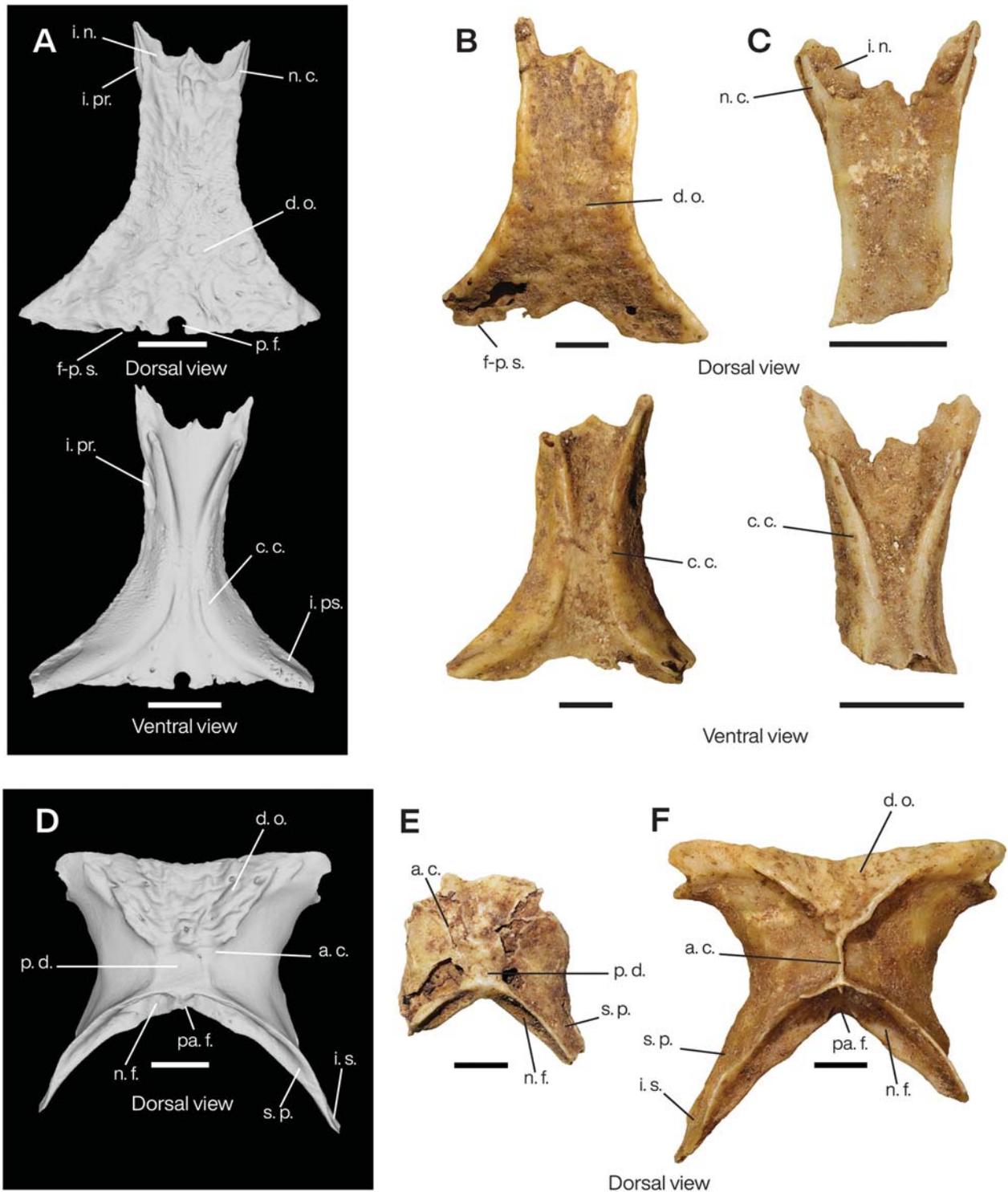
### **Parietal bone**

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

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



**FIGURE 4.** Premaxilla and maxilla of *Leiocephalus roquetus* sp. nov. A: 3D Model of the premaxilla of the holotype (MHNbX 2002.1871); B: Paratype “PGR6. square C11c. *décapage* 14.XII” collected in PGR6 deposit. C: 3D Model of the right maxilla of the holotype (MHNbX 2002.1871); D: Paratype “PGR6. square B10d. *décapage* 22.III” (right) collected in PGR6 deposit. **Abbreviations:** c. i. p. p.: crest of the internal premaxillary process, e. p. p.: external premaxillary process, f. p.: facial process, f. t. t.: first most anterior tricuspid tooth, i. m.: imprint of the maxilla, i. n.: imprint of the nasal bone, i. p.: incisive process, i. p. p.: internal premaxillary process, m. p.: maxillary process, n. p.: nasal process, p. f.: premaxillary fenestra, s. s.: supradental shelf, z. p.: zygomatic process. Scale bars= 2mm.



**FIGURE 5.** Frontal and parietal bones of *Leiocephalus roquetus* sp. nov. A: 3D Model of the frontal bone of the holotype (MHNbx 2002.1871); B: Paratype frontal bone “PGR6. square B10d. *décapage* 13.IV” collected in PGR6 deposit; C: Paratype frontal bone “PGR6. square B10d. *décapage* 13.V” collected in PGR6 deposit; D: 3D Model of the parietal bone of the holotype (MHNbx 2002.1871); E: Paratype parietal bone “PGR6. square C11d. *décapage* 12.VI” collected in PGR6 deposit; F: Paratype parietal bone “PGR6. square B9b. *décapage* 22.VII” collected in PGR6 deposit. **Abbreviations:** a. c.: adductor crest, c. c.: cranial crest, d. o.: dermal ornamentation, f-p. s.: fronto-parietal suture, i. n.: imprint of the nasal bone, i. pr.: imprint of the prefrontal bone, i. ps.: imprint of the postfrontal bone, i. s.: imprint of the supratemporal bone, n. c.: nasal process crest, n. f.: nuchal fossa, pa. f.: parietal fossa, p. d.: postero-medial depression, p. f.: parietal foramen, s. p.: supratemporal process. Scale bars=2mm.

“PGR6. square B9b. *décapage* 22.VII” (Fig. 5–F): This bone was found in layer 4 of PGR6 (square B9b, *décapage* 22). This element is a nearly complete parietal in a more advanced ontogenetic stage than the holotype and paratype described above. It is larger than the other parietal bones we identified, with a maximal antero-posterior length of 12.3 mm. While similar to the holotype, the morphology of the parietal table and adductor crests is completely different. In addition to being high and well defined, the crests delimit a V-shape ornamented area and meet in the posterior part of the bone to form a single crest reaching the postero-medial extremity of the parietal table.

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

### **Pterygoid bone**

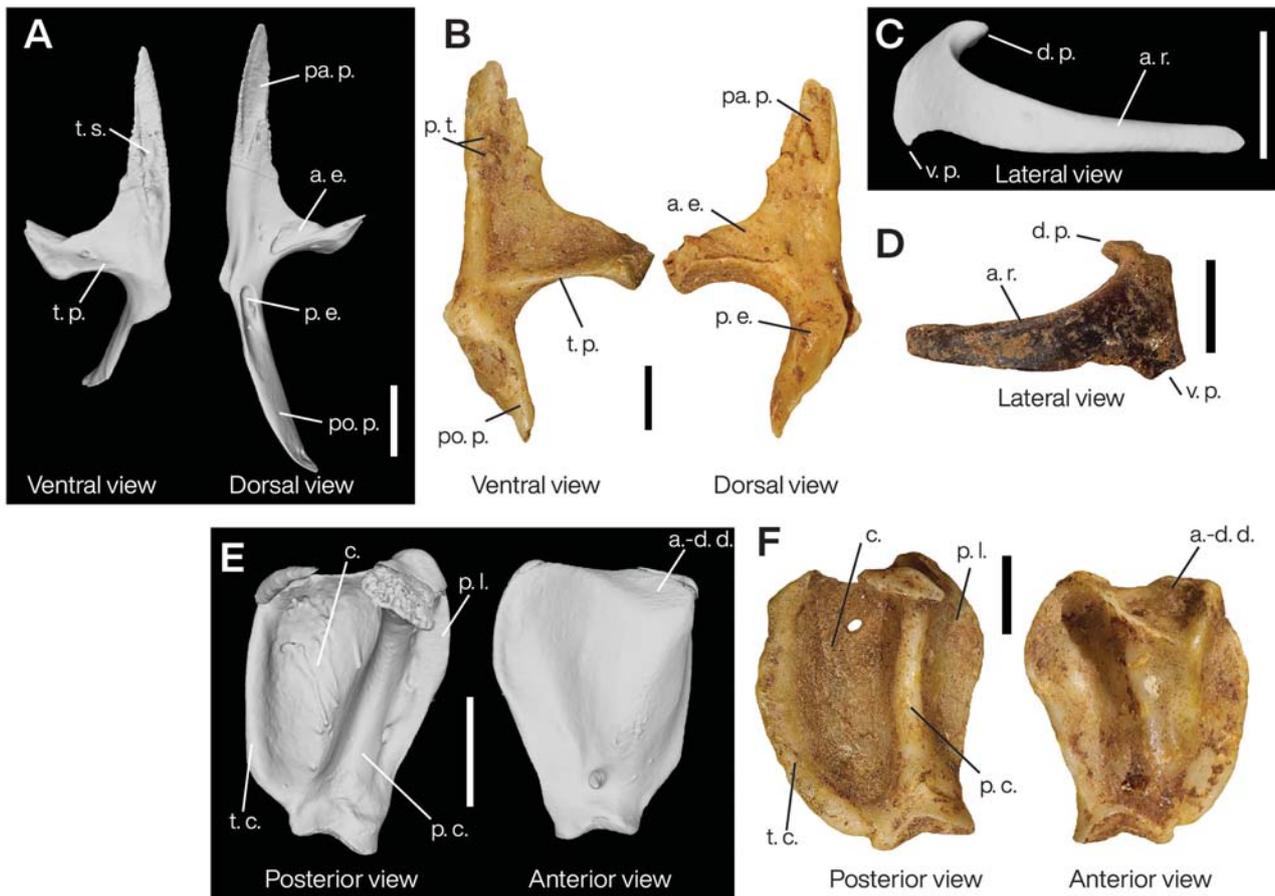
**Holotype** (MHNbX 2002.1871) (Fig. 6–A): The bone presents a long, thin posterior process accounting for half of the length of the complete bone. In dorsal view, the transverse process extends moderately laterally and bears a well-marked, triangular articular surface with the ectopterygoid. The base of the posterior process has a deep pit for the insertion of the epipterygoid bone. In dorsal view, the palatine process forms a long and relatively thin blade whose pointed anterior tip bears a well-defined contact area with the palatine bone. In medial view, the anterior extremity of the posterior process presents a deep indentation occupied by a well-marked articular surface for the basiptyergoid process of the basisphenoid bone. Posteriorly to this structure, an oval pterygoid furrow occupies most of the medial area of the posterior process. In ventral view, the palatal process present superficial traces of teeth sockets (*sensu* Mahler & Kearney 2006), and two teeth were present on the left pterygoid of the holotype specimen. However, these teeth were not attached to the bone by any ossified structure and were absent on the right pterygoid. It is therefore difficult to be certain if the absence of pterygoid teeth is a general trait of *L. roquetus* as this character could reflect intra-individual and intra-specific variability. Such variability was previously observed by Mahler & Kearney (2006) in the genus *Leiocephalus*.

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

### **Squamosal bone**

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

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



**FIGURE 6.** Pterygoid, squamosal and quadrate bones of *Leiocephalus roquetus* **sp. nov.** A: 3D Model of the right pterygoid of the holotype (MHNbx 2002.1871); B: Paratype left pterygoid bone “PGR6. square C11d. *décapage* 14.X” collected PGR6 deposit; C: 3D Model of the right squamosal of the holotype (MHNbx 2002.1871); D: Paratype left squamosal bone “PGR6. square B9b. *décapage* 22.IX” collected in PGR6 deposit; E: 3D Model of the left quadrate of the holotype (MHNbx 2002.1871); F: Paratype left quadrate bone “PGR6. square C11c. *décapage* 15.XI” collected in PGR6 deposit. **Abbreviations:** a.-d.d.: antero dorsal depression, a.e.: articular surface with the ectopterygoid bone, a.p.: articular surface with the palatine bone, a.r.: anterior ramus, c.: conch, d.p.: dorsal process, p.c.: posterior crest, p.e.: pit for the insertion of the epipterygoid, p.l.: pterygoid lamina, p.t.: pterygoid teeth?, pa.p.: palatine process, po.p.: posterior process, t.c.: tympanic crest, t.p.: transverse process, t.s.: tooth socket, v.p.: ventral process. Scale bars= 2mm.

### **Septomaxilla**

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

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

### **Quadrate bone**

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

**Paratypes:** “PGR6. square C11c. *décapage* 15.XI” (Fig. 6–F): This bone comes from layer 3 of PGR6 (square

C11c, *décapage* 15). This bone is similar to the holotype but is larger (7.7 mm high) and its antero-dorsal depression is more strongly marked and delimited than in the holotype which could reflect ontogenetic variability.

### **Dentary**

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

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

“PGR6. square C11c. *décapage* 11.II” (Fig. 7–C): This bone is a nearly complete subfossil dentary missing its posterior extremity and whose anterior part is dissolved, probably due to it being digested just as several other bone remains in the fossil assemblage presenting characteristic marks of digestion (Fernández-Jalvo & Andrews 2016). This bone was also found in layer 3 of PGR6 layer (square C11c; *décapage* 11) and exhibits a similar dental length (14.4 mm) and number of teeth (n=25) to the holotype.

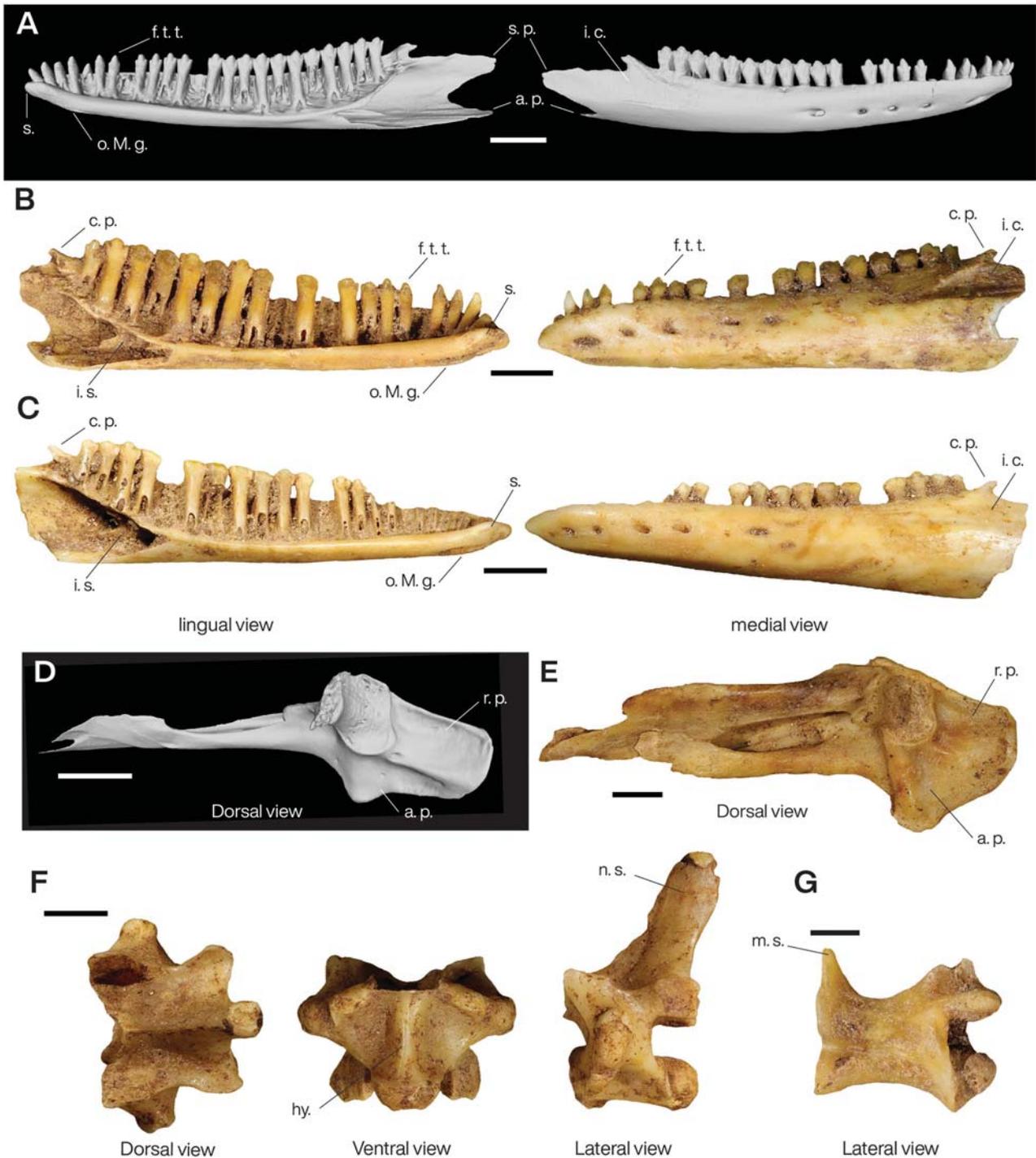
**Additional material:** Two additional but less well-preserved dentaries were also recovered from PGR6. Dental rows measure 14.7 mm and 12 mm and bear, respectively, 21 and 20 tooth positions. The smallest dentary presents a juvenile morphology and the most anterior tricuspid tooth occupies the sixth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

### **Articular**

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

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

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



**FIGURE 7.** Dentary, articular bones and vertebrae of *Leiocephalus roquetus* **sp. nov.** A: 3D Model of the right dentary of the holotype (MHNbx 2002.1871); B: Paratype dentary “PGR6. square C11d. *décapage* 16.I” (left) collected in PGR6 deposit; C: Paratype dentary “PGR6. square C11c. *décapage* 11.II” (left) collected in PGR6 deposit; D: 3D Model of the right articular of the holotype (MHNbx 2002.1871); E: Paratype articular “PGR6. square B9b. *décapage* 17.VIII” (right) collected in PGR6 deposit; F: Anterior trunk vertebra collected in the layer 4 of PGR6 (square B10d, *décapage* 20); G: Caudal vertebra collected in the layer 2/3 of PGR6 (square B10d, *décapage* 10). **Abbreviations:** a. p.: angular process, c. p.: coronoid process, f. t. t.: first most anterior tricuspid tooth, hy.: hypapophysis, i. c.: lateral imprint of the coronoid bone, i. s.: intra-mandibular septum, m. s.: medial spine, n. s.: neural spine, o. M. g.: anterior opening of the Meckelian groove, r. p.: retroarticular process, s.: symphysis, sy.: synapophysis, s. p.: surangular process. Scale bars=2 mm.

Additional remarks regarding fossil post-cranial elements: In addition of the cranial elements described above, the PGR6 deposit produced several postcranial elements of *Leiocephalus* that we attribute to *L. roquetus*. However, as comparing these elements with the holotype specimen was impossible, we describe their main morphological characters without considering these bones as type material.

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

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

### **General remarks**

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

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

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

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

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

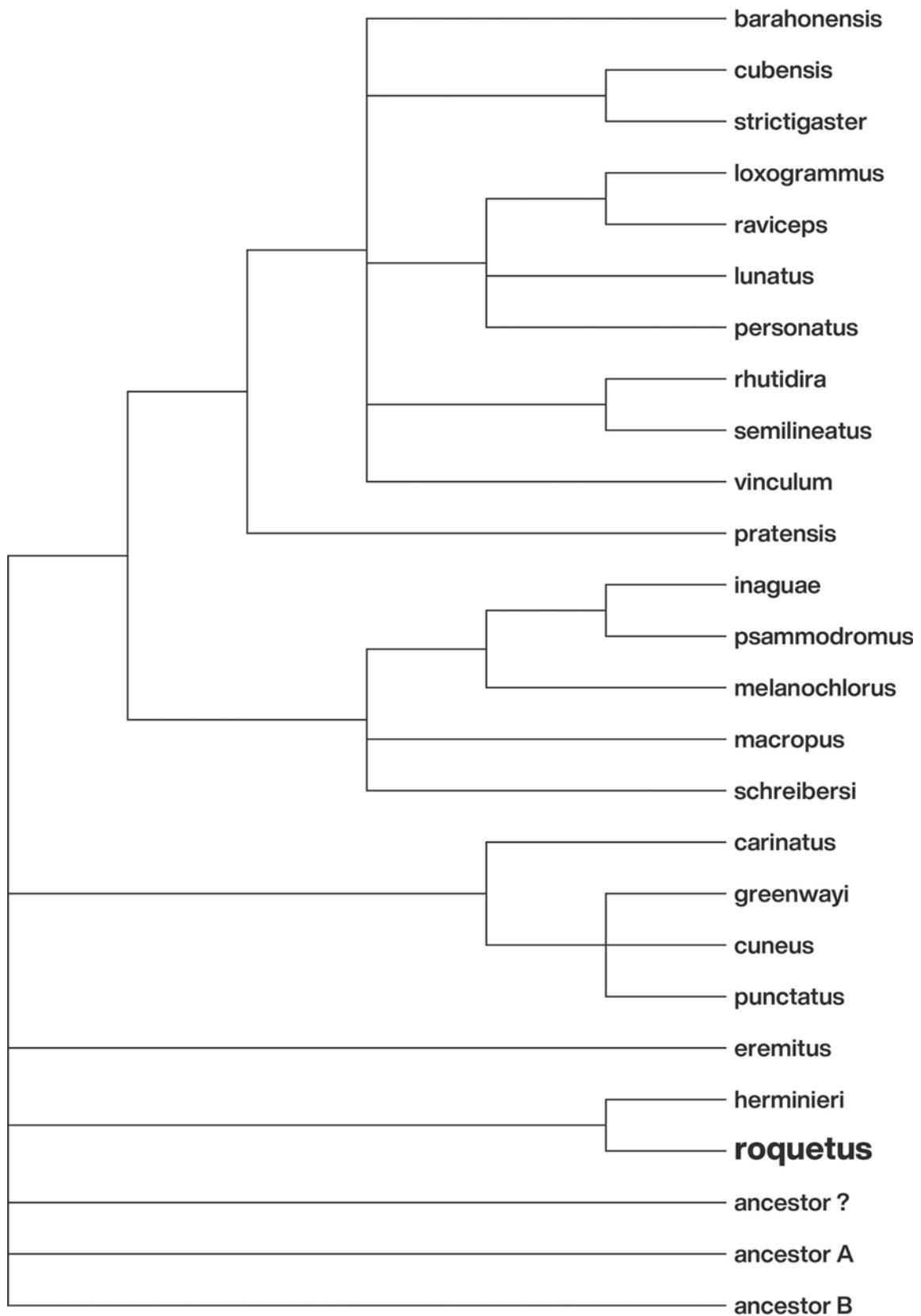
In terms of the size of *L. roquetus*, although the holotype specimen is moderate in size (snout-vent length of 10.8 cm), most of the fossil bones attributed to this species were larger, indicating that the type specimen is likely to be a juvenile. Isolated bones do not, however, provide direct evidence for the size of the complete specimen, and we can only provide a rough estimate of the putative size of adult *L. roquetus*. The fossil bones from PGR6 are of similar size to the largest bones reported by R. Etheridge (1964) to estimate the size of *L. cuneus* (200 mm SVL). Certain elements are both smaller (premaxilla, quadrate, dentary, articular) or larger (maxilla, frontal, parietal), leading us to estimate *L. roquetus* to be roughly of similar size as *L. cuneus*, which is currently the largest known *Leiocephalus* species.

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

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

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

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



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

## Discussion

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

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

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

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

The lack of dated fossils and their rarity raises two possibilities; 1) *Leiocephalus* species were almost entirely extinct more than two thousand years ago and are thus logically absent from Lesser Antillean archaeological deposits that predate the human colonization of the islands or, 2) their absence reflects biases in the identification of fossil remains or the composition of faunal assemblages from open-air archaeological deposits. These issues are not specific to *Leiocephalus*, as recently demonstrated by the similar complete absence of *Boa* snakes in regional archaeological sites, pattern which has potentially been linked to specific Amerindian cultural practices (Bochaton 2020). A similar lack of past occurrence data was also used to support an early Holocene extinction of *Diploglossus* in the Lesser Antilles (Underwood 1964; although see Bochaton *et al.* 2016 for rare archaeological data contradicting this position). It is possible that the small size and relative morphological similarity with other lizard bones renders identifying *Leiocephalus* specimens from archaeological deposits difficult. In this respect, it is interesting to note that rare archaeological taxa, such as *Leiocephalus* (Bailon *et al.* 2015; Boudadi-Maligne *et al.* 2016; Kemp & Hadly 2016; Pregill *et al.* 1994; Roughgarden & Pacala 1989; Stouvenot *et al.* 2014; Watters *et al.* 1984), *Boa* (Bochaton 2020; Bochaton & Bailon 2018), and *Diploglossus* (Bochaton *et al.* 2016), were mentioned only by trained paleo-herpetologists. This lack of archaeological data concerning *Leiocephalus* is thus not a good argument for their absence during the Amerindian and historical periods. These lizards might have disappeared during the 19<sup>th</sup> century colonial period, which would explain why they were overlooked by the biologists who provided the first descriptions of fauna in the West Indies.

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

The geological history of the West-Indies is complex as the geography of this area, especially its southern part, has undergone massive changes across the last 50 million years. The West-Indies have been mainly colonized in Late Eocene to early Oligocene times from South America (Blackburn *et al.* 2020; Delsuc *et al.* 2019) thanks to a land bridge linking the Greater Antilles to the continent (Iturralde-Vinent 2006; Marivaux *et al.* 2020). This landmass however disappeared in the Late Oligocene while a much younger chain of islands emerged eastward (the modern Lesser Antilles) (Philippon *et al.* 2020). As an effect of this rich geological history several events can be drawn to explain the colonization of the Lesser Antillean islands with overwater dispersal events from South America, the Greater Antilles, or another still visible or nowadays disappeared island. Regarding *Leiocephalus*, hypotheses of its initial colonization of the Lesser Antilles vary according to the phylogenetic position of this genus. These lizards were first considered as “Tropiduridae” (Frost & Etheridge 1989) native to South America, prior to being found to be closer to North American genera (Hedges 1996). Recent molecular data indicates Leiocephalidae to be either a basal pleurodont squamate (Pyron *et al.* 2013) or a sister taxon to all pleurodont squamates (Zheng & Wiens 2016), making it difficult to pinpoint where they first appeared in the West Indies. Leiocephalidae and other pleurodont squamates diverged 91 My years ago (Zheng & Wiens 2016), which would considerably predate the K/T crisis and the divergence time of all Antillean taxa (Hedges 2006). Given the current absence of molecular data for Lesser Antillean *Leiocephalus*, it is difficult to evaluate the reliability of our morphology-based cladistic analysis. In addition, considering the changing position of Leiocephalidae since the initial work of Pregill (1992), it is also possible that the character states identified as “primitive” or “derived” need to be reevaluated in light of the past phylogenetic position of *Leiocephalus*. This renders interpreting our results concerning the existence of a basal Lesser Antillean clade more complex. Despite these uncertainties, if we accept the phylogenetic proximity between *L. herminieri* and *L. roquetus*, and a basal position in their genus clade, our results would suggest an initial colonization of the Cenozoic Antilles from South America just as it is the case for most other terrestrial taxa. However, in the absence of molecular data for each modern species and fossil data predating the Late Pleistocene for most of the West Indies, it is currently impossible to integrate this potential scenario within what is likely to be very old and complex colonization that included multiple extinction events. The history of *Leiocephalus* in the West Indies is probably significantly more complex than the majority of modern taxa, rodents for example (Marivaux *et al.* 2020) which colonized the region following either the formation of the Aves Ridge during the Oligocene or who dispersed after the emergence of the modern islands (Hedges 2006).

## Conclusion

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

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Appendix 1 Character matrix used in the phylogenetic analysis

Nº Caract/taxon	1	2	3	4	5	6	7	8	9	10
<i>barahonensis</i>	1	0	0	0	0	0	0	0	1	0
<i>carinatus</i>	?	0	0	0	?	0	0	0	0	0
<i>cubensis</i>	1	0	0	0	0	0	0	0	0	0
<i>eremitus</i>	?	?	?	?	?	?	?	?	?	?
<i>greenwayi</i>	0	0	0	0	1	0	0	1	0	0
<i>herminieri</i>	0	0	0	0	1	1	0	0	0	0
<i>inaguae</i>	0	1	1	0	0	0	1	1	0	0
<i>loxogrammus</i>	0	0	0	0	1	1	0	1	?	?
<i>lunatus</i>	1	0	0	1	0	0	0	0	0	0
<i>macropus</i>	1	1	0	0	1	0	1	0	0	?
<i>melanochlorus</i>	1	0	0	0	0	1	1	0	0	1
<i>personatus</i>	1	0	0	0	?	0	0	0	0	0
<i>pratensis</i>	1	0	0	0	0	0	1	0	0	0
<i>psammomodromus</i>	0	1	1	0	0	1	1	1	1	1
<i>punctatus</i>	0	1	0	0	1	0	1	1	0	0
<i>raviceps</i>	1	0	0	0	0	0	0	0	0	0
<i>rhutidira</i>	1	0	0	1	1	0	0	0	0	0
<i>schreibersi</i>	1	1	0	0	0	0	0	0	0	0
<i>semilineatus</i>	1	0	0	1	0	0	0	0	1	0
<i>sirictigaster</i>	1	0	0	0	0	0	0	0	0	0
<i>vinculum</i>	1	0	0	0	0	0	0	0	1	0
<i>roquetus</i> - Bordeaux	0	1	0	0	1	0	0	3	0	1
<i>roquetus</i> - Fossile	0	1	0	?	1	?	0	3	?	1
<i>cuneus</i>	?	0	0	?	1	?	0	1	?	?
ancestor ?	0	0	0	0	?	0	0	0	0	0
ancestor A	0	0	0	0	0	0	0	0	0	0
ancestor B	0	0	0	0	1	0	0	0	0	0

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## Appendix 1 (continued)

Nº	Caract/taxon	11	12	13	14	15	16	17	18	19	20
	<i>barahonensis</i>	1	1	0	0	0	3	0	3	0	1
	<i>carinatus</i>	?	0	0	?	0	2	1	3	0	1
	<i>cubensis</i>	1	1	0	0	0	2	0	2	0	1
	<i>eremitus</i>	?	?	0	?	?	1	0	3	0	1
	<i>greenwayi</i>	1	0	0	0	0	2	1	3	0	1
	<i>herminieri</i>	1	0	0	0	0	1	0	1	0	0
	<i>inaguae</i>	0	0	0	0	0	2	0	1	0	1
	<i>loxogrammus</i>	0	1	0	?	1	3	0	2	1	1
	<i>lunatus</i>	1	0	0	0	?	3	0	2	1	1
	<i>macropus</i>	0	0	0	0	0	2	0	1	0	2
	<i>melanochlorus</i>	0	0	0	0	0	1	0	1	0	2
	<i>personatus</i>	1	1	0	0	1	3	0	2	0	1
	<i>pratensis</i>	0	0	0	0	0	3	0	3	0	2
	<i>psammodromus</i>	0	0	0	0	0	1	0	1	0	?
	<i>punctatus</i>	0	0	0	0	0	2	1	3	0	1
	<i>raviceps</i>	1	1	0	1	1	3	0	2	1	1
	<i>rhuiddira</i>	1	1	1	0	0	3	0	2	0	1
	<i>schreibersi</i>	0	1	0	1	0	2	0	1	0	1
	<i>semilineatus</i>	1	1	0	0	0	3	0	2	1	1
	<i>strictigaster</i>	1	1	0	0	0	2	0	2	0	1
	<i>vinculum</i>	0	1	0	0	0	3	0	2	0	1
	<i>roquetus</i> - Bordeaux	1	1	0	?	?	1	0	1	0	1
	<i>roquetus</i> - Fossile	1	?	0	0	0	?	?	?	?	?
	<i>cuneus</i>	1	0	1	?	?	?	?	?	?	?
	ancestor ?	0	0	0	0	0	0	0	0	0	0
	ancestor A	0	0	0	0	0	0	0	0	0	0
	ancestor B	0	0	0	0	0	0	0	0	0	0

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## Appendix 1 (continued)

Nº Caract/taxon	21	22	23	24	25	26	27	28	29	30
<i>barahonensis</i>	0	0	1	0	0	0	1	0	1	2
<i>carinatus</i>	0	0	0	0	0	0	1	0	0	1
<i>cubensis</i>	0	2	0	0	0	0	1	0	1	0
<i>eremitus</i>	1	0	0	0	1	0	1	0	?	1
<i>greenwayi</i>	0	0	0	0	1	1	1	1	0	0
<i>herminieri</i>	0	0	0	0	1	0	0	0	0	0
<i>inaguae</i>	0	0	0	0	1	1	1	1	1	0
<i>loxogrammus</i>	0	1	0	1	0	0	1	0	1	0
<i>lunatus</i>	0	1	0	0	0	0	0	0	1	0
<i>macropus</i>	0	2	0	0	1	1	1	0	1	0
<i>melanochlorus</i>	1	2	0	0	1	1	1	0	0	0
<i>personatus</i>	0	1	0	0	0	0	0	0	1	?
<i>pratensis</i>	0	1	0	0	0	0	2	0	1	1
<i>psammodromus</i>	1	0	0	0	1	1	1	1	?	0
<i>punctatus</i>	1	0	0	0	1	0	1	0	0	0
<i>raviceps</i>	0	2	0	1	0	0	1	1	1	0
<i>rhutidira</i>	0	0	1	0	0	0	1	0	2	0
<i>schreibersi</i>	0	1	0	0	1	1	1	1	1	0
<i>semilineatus</i>	0	0	1	0	0	0	1	0	1	0
<i>strictigaster</i>	0	2	0	0	0	0	1	0	1	0
<i>vinculum</i>	0	0	0	0	0	0	1	0	0	?
<i>roquetus</i> - Bordeaux	0	0	0	0	1	0	0	0	?	0
<i>roquetus</i> - Fossile	?	?	?	?	?	?	?	?	?	?
<i>cuneus</i>	?	?	?	?	?	?	?	?	?	?
ancestor ?	0	0	0	0	?	?	?	?	0	?
ancestor A	0	0	0	0	0	0	0	0	0	0
ancestor B	0	0	0	0	1	1	1	1	0	1

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## Appendix 1 (continued)

Nº Caract/taxon	31	32	33	34	35	36	37	38	39	31
<i>barahonensis</i>	2	0	1	0	0	0	0	0	0	2
<i>carinatus</i>	1	0	2	0	0	0	0	0	0	1
<i>cubensis</i>	1	0	2	0	0	0	0	1	0	1
<i>eremitus</i>	0	0	2	0	0	0	0	0	0	0
<i>greenwayi</i>	1	0	2	0	0	1	0	0	0	1
<i>herminieri</i>	0	0	3	0	0	0	0	0	1	0
<i>inaguae</i>	0	0	3	1	0	0	1	0	1	0
<i>loxogrammus</i>	1	0	2	0	0	0	0	2	0	1
<i>lunatus</i>	1	0	2	0	0	1	0	0	0	1
<i>macropus</i>	0	1	3	1	0	1	0	2	0	0
<i>melanochlorus</i>	0	0	3	1	0	0	1	0	1	0
<i>personatus</i>	1	0	2	0	0	0	0	1	0	1
<i>pratensis</i>	2	0	1	0	0	0	0	2	0	2
<i>psammodromus</i>	0	0	3	1	0	0	1	0	1	0
<i>punctatus</i>	1	0	2	0	0	0	0	0	0	1
<i>raviceps</i>	1	0	2	1	0	0	0	2	0	1
<i>rhutidira</i>	1	0	2	0	0	0	0	0	0	1
<i>schreibersi</i>	0	1	3	1	1	0	0	0	0	0
<i>semilineatus</i>	1	0	2	0	0	0	0	2	0	1
<i>strictigaster</i>	1	0	2	0	0	0	0	0	0	1
<i>vinculum</i>	2	0	2	0	0	0	0	0	0	2
<i>roquetus</i> - Bordeaux	?	?	?	?	0	0	0	0	1	?
<i>roquetus</i> - Fossile	?	?	?	?	?	?	?	?	?	?
<i>cuneus</i>	?	?	?	?	?	?	?	?	?	?
ancestor ?	0	0	0	0	0	0	0	?	0	0
ancestor A	0	0	0	0	0	0	0	0	0	0
ancestor B	0	0	0	0	0	0	0	1	0	0