

1 **Archaeobiogeography of extinct rice rats (*Oryzomyini*) in the**  
2 **Lesser Antilles during the Ceramic Age (500 BCE to 1500 CE)**

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1 **ABSTRACT**

2       During the Ceramic Age (500 BCE – 1500 CE), Lesser Antilles rice rats (Tribe Oryzomyini)  
3 made up a significant portion of the diet of Caribbean islanders. Archaeological excavations  
4 across the archipelago resulted to the discovery of large quantities of remains from to these now  
5 extinct taxa. It offers a unique opportunity to investigate the past biogeography of this taxon of  
6 high cultural and ecological importance. We have studied 1140 first lower molars originating  
7 from 40 archaeological sites across eleven islands of the Lesser Antilles archipelago using two-  
8 dimensional geometric morphometric approaches to establish spatiotemporal patterns relying  
9 on phenotypic variations. This study identified three morphological groups, present in all  
10 chrono-cultural periods, that were geographically restricted and consistent with published  
11 ancient mitochondrial DNA clusters. These three geographically-separate groups likely  
12 represent three distinct genera of rice rats. The first group includes specimens from the North  
13 of the archipelago (Saint-Martin, Saba, Saint-Eustatius, Saint-Kitts and Nevis) and likely  
14 referable to as *Pennatomys* sp.; the second, occurring in the South (Martinique), is assigned to  
15 *Megalomys desmarestii*; and the third corresponds to specimens from the center of the Lesser  
16 Antilles (Antigua, Barbuda, Marie-Galante and Guadeloupe) and likely corresponds to  
17 *Antillomys* sp. These oryzomyine morphotypes are present during all studied periods and  
18 support an older presence of these rodents in the region. Our results are congruent with ancient  
19 DNA studies that favor the hypothesis of a natural introduction of the group in the archipelago  
20 before settlement of human populations. Moreover, the observed phenotypic homogeneity and  
21 stability over the 2000 years of Pre-Columbian occupation suggests that rice rats were not part  
22 of long-distance inter-island exchanges by humans. Instead, rice rat human consumption was  
23 likely based on in-situ hunting of local populations.

24

1 **Keywords:** Caribbean archipelago – Bioarchaeology – Geometric morphometrics – Human  
2 colonization – Island evolution – Late Holocene – Rodents – Teeth

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4

## 5 **1. INTRODUCTION**

6 The Lesser Antilles are an oceanic archipelago in the Caribbean, located between two  
7 biogeographic features, the Anegada passage off the Anguilla bank (Jany et al., 1990), and  
8 Koopman's Line off the Grenada Bank (Genoways et al., 2010) (Fig. 1). The Lesser Antilles  
9 show a low diversity of terrestrial organisms associated with a high rate of endemism common  
10 to many island ecosystems (e.g. Baker & Genoways, 1978; Bond, 1999; Hedges, 1999; Ricklefs  
11 & Bermingham, 2007) which are profoundly influenced by both modern and past human  
12 activity (Whittaker and Fernández-Palacios, 2007). The first attested human settlement in the  
13 Lesser Antilles dates to the 4<sup>th</sup> millennium BCE (Bonnissent et al., 2014) in Saint-Martin.  
14 Archaeological records confirm the ancient introduction and translocation of continental plants  
15 and animals that are still present today, including manioc (*Manihot exculenta*), maize (*Zea*  
16 *mays*), papaya (*Carica papaya*) (Newsom and Wing, 2004; Pagán Jiménez et al., 2005), dogs  
17 (*Canis familiaris*), and agouti (*Dasyprocta* sp.) (Bonnissent, 2008; Giovas et al., 2012, 2016;  
18 Wing, 2001a). Lesser Antillean rice rats (tribe Oryzomyini) are considered to be endemic to the  
19 archipelago, as the timing of their arrival in this area has been estimated via molecular clock  
20 analysis to the Late Miocene (6.814-6.303 Mya - Brace, Turvey, Weksler, Hoogland, & Barnes,  
21 2015). However, the oldest secure evidence of rice rats recovered from the paleontological  
22 record is contemporaneous with the earliest human occupations of the archipelago (Steadman  
23 et al., 1984). Rice rats are abundant in archaeological assemblages and show clear evidence of  
24 consumption (cutting and burning marks) (Grouard, 2007), though are now extinct across the  
25 Lesser Antilles, with the last living specimen recorded during the mid-late 19<sup>th</sup> century (Allen,

1 1942; Ray, 1962). Traditional reasons for small mammal extinction on islands include the  
2 introduction of competing species (MacPhee and Flemming, 1999) such as rats (*Rattus rattus*  
3 and *R. norvegicus*) or new predators like the cat (*Felis silvestris*) (Henderson, 1992), the Small  
4 Indian mongoose (Herpestidae, *Urva auropunctata*) (Grouard, 2001; Henderson, 1992; Horst  
5 et al., 2001) and the racoon (Procyonidae, *Procyon lotor*) (Louppe et al., 2020), or overhunting  
6 (Ray, 1962; Steadman et al., 1984; Trouessart, 1885), along with the transformation of the  
7 landscapes and deforestation (Boudadi-Maligne et al., 2016). Yet the specific causes of rice rat  
8 extinction in the Lesser Antilles still remains unclear.

9 Pre-Columbian societies relied primarily on marine resources such as fish and mollusks  
10 (Grouard, 2010; Wing and Wing, 1995) but terrestrial mammals, including oryzomyines, were  
11 also consumed as evidenced by the presence of butchery and burning marks on recovered  
12 remains (Grouard, 2004, 2010; Newsom and Wing, 2004; Wing, 2001b, 2001a). Rice rats were  
13 an important part of the human diet throughout the Ceramic Age. Analysis of zooarchaeological  
14 collection from the site of Hope Estate (Saint-Martin) show that rice rats comprise 54% of the  
15 total number of all identified vertebrates (NMI=748/1,384; Grouard, 2004). Extensive evidence  
16 for anthropic inter-island exchange in the Lesser Antilles has been evidenced for e.g. dogs,  
17 humans, raw materials, and artefacts (i.e. Bonnissent, 2008; Bonnissent, 2013; Fitzpatrick,  
18 2015; Hofman et al., 2006, 2007, 2008; Hofman and Hoogland, 2011; Knippenberg, 2007;  
19 Laffoon et al., 2013, 2015, 2016; Stouvenot and Randrianasolo, 2013). It is still unclear whether  
20 rice rats were part of this network. Anthropic translocation has been proposed for the group  
21 (LeFebvre and deFrance, 2014) and exemplified by the presence of South American rice rats  
22 of the genus *Zygodontomys* in the island of Carriacou (Giovas, 2018; Mistretta, 2019).

23 Rodents have colonized a remarkable number of islands worldwide, either by natural  
24 dispersal (e.g. Fabre et al., 2013; Jansa et al., 2006), as stowaway like the black rat (*Rattus*  
25 *rattus*; MacPhee and Flemming, 1999; Vigne and Valladas, 1996) or intentional transportation

1 like the domestic guinea pig (*Cavia porcellus*; Kimura et al., 2016; LeFebvre and deFrance,  
2 2014; Lord et al., 2018). Morphological similarities between rodent populations can be used to  
3 explore the type of dispersal (e.g. Cucchi et al., 2014; LeFebvre et al., 2019) along with the  
4 impact of environmental factors on their diversity (e.g. Maestri et al., 2018).

5 In this study we have used tooth identification as the basis of our analysis. Teeth have an  
6 advantage over other skeletal elements in that they are often well preserved, are recovered in  
7 large numbers in the archaeological record and known to be taxonomically informative (Cucchi,  
8 2009; Darviche et al., 2006; Darviche and Orsini, 1982; Renaud et al., 1996; van Dam, 1996).  
9 Consequently, teeth, especially their size and shape have been used to study past rodent  
10 populations and their relationship with human societies (e.g. Cucchi et al., 2014; Hulme-  
11 Beaman et al., 2018b; Valenzuela-Lamas et al., 2011).

12 Because Lesser Antilles rice rats have no direct modern relatives and because  
13 morphological evolution of insular populations can happen very fast (Millien, 2006) eventually  
14 leading to inter-island radiation (e.g. Kadmon and Allouche, 2007), the current systematic and  
15 taxonomy of the group is still not fully established. Three genera are currently recognized in  
16 the Lesser Antilles archipelago (Brace et al., 2015; Machado et al., 2014) (Fig. 1): *Pennatomys*  
17 has been described in the North of the archipelago (Saint-Eustatius, Saint-Kitts and Nevis)  
18 (Turvey et al., 2010), *Megalomys* (Trouessart, 1885) in the South (Martinique, Saint-Lucia and  
19 Barbados) (Forsyth Major, 1901; Friant, 1941; Miljutin, 2010), and *Antillomys* (Brace et al.,  
20 2015) in the center (Guadeloupe, Antigua and Barbuda) (Barbotin, 1970; Brace et al., 2015;  
21 Hopwood, 1926; Pregill et al., 1994). These three genera are supported by high genetic  
22 divergence (560 bp of the Cytochrome b gene) and according to ancient genetic data  
23 *Megalomys* and *Pennatomys* are sister clades, only distantly related to the genus *Antillomys*  
24 (Brace et al., 2015). The present study aims to assess the archaeobiogeography of the  
25 oryzomyines taxa in the Lesser Antilles during the Ceramic Age and explore whether spatio-

1 temporal variation in their morphology can be explained through human translocation. Results  
2 were compared to published ancient DNA clusters in order to gain in the understanding on the  
3 group taxonomy.

4

5 <Figure 1>

6

## 7 **2. MATERIALS**

### 8 ***2.1 Chrono-cultural division***

9 The pre-Columbian archaeology of the Lesser Antilles is divided into two main periods: the  
10 Early and Late Ceramic Ages, each further divided into an early and a late phase. The Early  
11 Ceramic Age corresponds to the Saladoid cultures and it is divided into an early phase A (ECA)  
12 dating from *c.* 500 BCE to 400 CE (Early Cedrosan Saladoid and Huecan Saladoid), and a late  
13 phase B (ECB) from *c.* 400 to 600/800 CE (modified Cedrosan Saladoid, Late Saladoid, and  
14 Saladoid with Barrancoid influences) (Bérard, 2012; Fitzpatrick, 2015; Hofman et al., 2007,  
15 2008). The Late Ceramic Age corresponds to the Troumassoid cultures and is divided into an  
16 A phase (LCA) dated from 600/800 to *c.* 1200 CE, and a B phase (LCB) dated from *c.* 1200 to  
17 1500 CE. Contrary to the Early Ceramic, the two phases of Late Ceramic were characterized  
18 by a geographic division between the North and the South of the archipelago (Crock and  
19 Petersen, 2004; Mol, 2006; Rouse and Faber Morse, 1999; Siegel, 1989). The LCA is  
20 characterized by the Northern Troumassan Troumassoid and the Southern Suazan  
21 Troumassoid, while the LCB correspond to the Marmoran Troumassoid in the North and  
22 Troumassan Troumassoid in the South.

23

### 24 ***2.2 Studied specimens***

25 A total of 1140 archaeological first lower molars (M<sub>1</sub>, either isolated or enclosed in the  
26 mandible) belonging to adult specimens with limited wear were analyzed. When teeth were not

1 found isolated, only hemi-mandibles were recovered and could not be left and right paired to  
2 form complete jaws based on tooth wear abrasion or stratigraphic information, as a consequence  
3 it is possible that both the right and left M<sub>1</sub> of some specimens were included in the analyses.  
4 Specimens originated from 40 archaeological sites spanning across the pre-Columbian Ceramic  
5 Age in eleven islands throughout the archipelago (Fig. 1; Table 1). Specimens were assigned  
6 to chronological cultural phases based on primary publications and excavation reports, and  
7 according to investigators' opinion (Table 1; SI.1).

8

9 <Table 1>

10

### 11 **3. METHODS**

#### 12 *3.1 Morphometrics*

13 Photographs of the occlusal view of the lower first molar were taken using a LEICA 76  
14 APO macroscope and a non-distorting objective, with a 1.25x or 1.6x magnification and Leica  
15 Microsystem LAS software (V4.8). A sliding semi-landmark based geometric morphometric  
16 approach was employed to quantify the size and the shape of the teeth. On each photograph,  
17 the two-dimensional coordinates of one landmark, placed at the junction between the most  
18 posterior point of the metaconid and the external buccal edge of the tooth were recorded, along  
19 with 65 equidistant sliding semi-landmarks localized along the external edge of the tooth  
20 (recorded clockwise) (Fig. 2) using TPS Dig2 (Rohlf, 2004). All photographs and  
21 measurements were taken by the same person (M.D.). Coordinates were superimposed using a  
22 generalized Procrustes analysis (GPA) (Goodall, 1995; Rohlf and Slice, 1990), with the semi-  
23 landmarks allowed to slide following the Procrustes distance minimization criterion. Analyses  
24 of size were based on the log-transformed centroid size, and investigation of shape performed  
25 on the Procrustes residuals (coordinates after superimposition).

26

1 <Figure 2>

2  
3 **3.1 Statistics**

4 Prior to analyses, the existence of size or shape clusters at each archaeological site, island,  
5 island bank, and overall was examined using a Gaussian Mixture Modelling for Model-Based  
6 Clustering (R package ‘mclust,’ Scrucca, 2016). This approach determines, based on a  
7 maximized loglikelihood approach, the number of clusters (i.e. groups) present in the dataset,  
8 without *a priori* knowledge.

9 Centroid size differences between populations from different sites, periods, islands and  
10 island banks were tested with Kruskal-Wallis and Wilcoxon tests and visualized by boxplots.  
11 In pairwise comparisons, p-values were adjusted using a Benjamini-Hochberg multi-  
12 comparison procedure (Benjamini and Hochberg, 1995).

13 The shape variation was examined through the application of principal component analysis  
14 (PCA), before testing differences between groups through multivariate analysis of variance  
15 (MANOVA). Because of the large number of variables compared to the relatively low number  
16 of specimens per group, a dimensionality reduction of the data was performed (Baylac and  
17 Friess, 2005; Evin et al., 2013). Canonical variate analysis (CVA) and MANOVAs were  
18 performed on the firsts PCA scores that maximized the between-group discrimination  
19 quantified by leave-one-out cross validation (Baylac and Friess, 2005; Dobigny et al., 2002).  
20 CVA was used to quantify and visualize the group differences (Albrecht, 1980; Gittins, 1985;  
21 Russell et al., 2000). The discrimination power of the CVA was quantified by the mean cross-  
22 validation percentage (CVP) and the 90% confidence interval obtained from 100 CVAs  
23 performed on resampled same-size datasets (Evin et al., 2013). This approach randomly sub-  
24 samples the largest groups to the size of the smallest group, thus removing effects of unbalanced  
25 sample size which is common and largely inevitable in bioarchaeology (Evin et al., 2013).  
26 Cross-validation percentages were calculated for size, shape and form (size+shape). In addition



1 to CVA, phenotypic dissimilarity between groups were assessed using both Mahalanobis and  
2 Procrustes distances. Distances were computed only for groups of at least 10 specimens and the  
3 repeatability of the topologies was estimated by bootstrap with 1000 replicates. Procrustes  
4 distances between group mean shape was obtained following Nagorsen and Cardini (2009) and  
5 Mahalanobis distances were obtained from resampled datasets with equal number of specimens  
6 per group. For both approaches the number of resampled specimens match the number of  
7 specimens in the smallest group. The majority-rule consensus and mean branch lengths  
8 topologies were computed as unrooted Neighbor-Joining (NJ) networks (Friesen et al., 2007;  
9 Saitou and Nei, 1987) on which the percentage of trees in which each observed node grouping  
10 appeared has been reported (i.e. bootstrap supports). All analyses were performed in R version  
11 3.5.3 (R Core Team, 2019), with the ‘ape’ (Paradis and Schliep, 2018), ‘Morpho’ (Schlager,  
12 2013) and ‘Geomorph’ (Adams et al., 2018) packages.

13

#### 14 **4. RESULTS**

15 None of the clustering analysis on size and shape revealed the presence of multiple groups.  
16 As a consequence, the composition of each archaeological site was considered homogeneous.  
17 Despite the fact that the number of teeth per site and chrono-cultural period was maximized by  
18 including right and left teeth, statistical analyses were highly constrained by the number of  
19 specimens per site and chrono-cultural period. As a precaution, a subset of analyses were  
20 performed for teeth of only one side (left) of the mandible and provide congruent results though  
21 based on much less groups (for homogeneity groups with less than 10 specimens were  
22 excluded). Analyses performed in this study were constraint by available archaeological data  
23 which range from an island with only one site occupied during one period (e.g Saint-Kitts) to  
24 islands occupied during all periods on multiple sites (e.g. Martinique).

25

#### 1        **4.1 Main archaeobiogeographic pattern**

2        Analysis of the populations from each site and each cultural time period revealed three  
3 geographically structured clusters (figs. 3 & 4).

4  
5 <Figure 3>

6  
7 <Figure 4 >

8  
9        Molar centroid size analysis revealed two main clusters, perfectly discriminated, with the  
10 specimens from the Northern islands (Saint-Martin, Saba, Saint-Eustatius, Saint-Kitts and  
11 Nevis) showing much smaller teeth than any other specimens from across the archipelago (Fig.  
12 3).

13        Shape analysis revealed differences between the populations ( $F(46,2238)=105.91$ ,  $p \leq 2.2e-$   
14 16). While Procrustes distances do not provide a resolved network topology (most bootstrap  
15 values are  $< 50\%$ ) (SI.2), Mahalanobis networks (Fig. 4, SI.2) revealed three perfectly  
16 supported clusters (100% bootstrap values) that are geographically structured. The first cluster  
17 corresponds to the northern islands (Saint-Martin, Saba, Saint-Eustatius, Saint-Kitts and Nevis),  
18 the second to the central islands (Barbuda, Antigua, Grande-Terre and Basse-Terre of  
19 Guadeloupe, and Marie-Galante) while the third correspond the southern island of Martinique.  
20 However, when working at the island scale (SI.2) the split between Martinique and the central  
21 islands is not supported, but because of the relatively long length of the Martinique branch and  
22 the high size differences between the two geographic clusters (Fig. 3) they were considered as  
23 valid morphometric and geographic entities. The paired *leave-one-out* cross validation between  
24 the three geographic clusters is high (94.4 %; CI: 92.9 - 95.9 %) confirming their  
25 morphometrical distinction. Moreover, when molar form is analyzed, combining size and shape  
26 data, this percentage reaches 99.7 % (CI: 99.3 - 100 %).

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## *4.2 Regional spatio-temporal patterns*

Variation within the three clusters was then investigated at different geographical and chronological scales by looking at the differences between island banks (during past low-stand sea levels occurrences), between islands and sites, and through the different cultural time periods.

### *4.2.1 The five northern Islands*

Populations from the five northern islands differ in both size ( $X^2=147.5$ ,  $df=4$ ,  $p\leq 2.2e-16$ ;  $CVP=35\%$ ( $CI:28.8-43.8\%$ );  $SI.3.2$ ) and shape ( $F(44-2528)=11.8$ ,  $p\leq 2.2e-16$ ;  $CVP=51.1\%$  ( $CI:41.3-58.8\%$ );  $SI.3.1-2$ ) (Fig. 5). The island structuring of the populations observed in the networks (Fig. 4 & 5) is also evidenced by pairwise comparisons ( $SI.3.2$ ). The differences between islands exceed the differences between cultural time periods despite the small number of populations available for comparison. Only Saint-Martin is represented by more than one period with sufficient specimens for a diachronic comparison. One site (Hope Estate) was occupied during the ECA and ECB, and the corresponding specimens differ only slightly in shape ( $F(4,517)=4$ ,  $p=3e-3$ ;  $CVP=55.7\%$  ( $CI:50.5-59.9\%$ )) and not in size ( $W=22975$ ,  $p=0.3$ ;  $CVP=49.1\%$  ( $CI:46.8-53.2\%$ )). On the other hand, differences between islands during the ECB are highly significant in both size ( $X^2=106.3$ ,  $df=3$ ,  $p\leq 2.2e-16$ ;  $CVP= 39.7\%$  ( $CI:29.7-48.4\%$ );  $SI.3.2$ ) and shape ( $F(24-1533)=15.5$ ,  $p\leq 2.2e-16$ ;  $CVP= 57.8\%$  ( $CI:40.9-65.7\%$ );  $SI.3.1-2$ ).

<Figure 5>

### *4.2.2 Martinique*

1 In Martinique, the populations differ in both size ( $X^2=19.5$ ,  $df=5$ ,  $p=0.0015$ ;  $CVP= 23.5\%$   
2  $CI:5.6-38.9\%$ ) and shape ( $F(85,355)=2.2$ ,  $p=4e-7$ ;  $CVP=27.9\%$  ( $CI:11.1-44.4\%$ )). Specimens  
3 from the Early and Late Ceramic differ in shape ( $F(14,64)=3.9$ ,  $p=8e-5$ ;  $CVP=71.7\%$  ( $CI:64.8-$   
4  $79.6\%$ );  $SI.4.1-2$ ), but not in size ( $W=707$ ,  $p=1$ ;  $CVP=35.2\%$  ( $CI: 3.6-51.9\%$ ),  $SI.4.2$ ). The  
5 specimens from the ECB populations do not differ in size ( $X^2= 4$ ,  $df=2$ ,  $p=0.1$ ) or shape  
6 ( $F(16,36)=1.7$ ,  $p=0.1$ ). During the LCB, there was no observed size difference, ( $W=257$ ,  
7  $p=0.94$ ), but shape varied ( $F(8,38)=2.6$ ,  $p=0.02$ ;  $CVP=64.5\%$  ( $CI:55.6-75\%$ )).

8

#### 9 *4.2.3 The five Central islands*

10 The populations from the central islands differ in both size ( $X^2=105.4$ ,  $df=4$ ,  $p<2.2e-16$ ;  
11  $CVP=32.6\%$  ( $CI:28.1-37.8\%$ )) and shape ( $F(100,1536)=4.4$ ,  $p\leq 2.2e-16$ ;  $44.7\%$  ( $CI:38.5-$   
12  $51.2\%$ )). Only populations from Barbuda and Guadeloupe Basse-Terre are clustered by islands  
13 (only one population was studied from Antigua) contrary to the populations from Grande-Terre  
14 and Marie-Galante (Fig. 6).

15

#### 16 **<Figure 6>**

17

18 Specimens from the two islands of the Barbuda bank (Antigua and Barbuda) differ from  
19 each other in shape ( $F(7,61)=3.1$ ,  $p=0.007$ ;  $CVA=65.6\%$  ( $CI:59.3-72.2\%$ );  $SI.5.1$ ) but not in  
20 size ( $W=454$ ,  $p=0.2$ ). Specimens from the three archeological sites from Antigua ( $SI.5.1-2$ ), all  
21 attributed to the LCA, differ in shape ( $F(16,36)=2.1$ ,  $p=0.03$ ;  $CVA=41.4\%$  ( $CI:22.2-66.7\%$ ))  
22 but not in size ( $X^2=1.49$ ,  $df=2$ ,  $p=0.47$ ). On Barbuda, the specimens from the two sites (one  
23 ECA, one LCA) do not differ in their molar size ( $W=170$ ,  $p\text{-value}=0.2$ ) nor shape ( $F(3,38)=0.3$ ,  
24  $p=0.9$ ).

1 Thirteen sites were analyzed from the Guadeloupe Bank (Basse-Terre + Grande-Terre,  
2 Table 1; SI.5.1-2). On average, specimens from Basse-Terre have larger molars than those from  
3 Grand-Terre ( $W=6398$ ,  $p=5.4e-11$ ,  $CVP=71.1\%$  (CI:68.8-73.6%)) and differ slightly in shape  
4 ( $F(15,169)=4.2$ ,  $p=1e-6$ ;  $CVP=50.2\%$  (CI:41.6%-58.4)). On Grande-Terre, the specimens from  
5 the different sites do not differ in size ( $X^2=5.5$ ,  $df=6$ ,  $p=0.5$ ), but differ in shape ( $F(78,588)=1.4$ ,  
6  $p=0.02$ ;  $CVP=28.4\%$  (CI:14.3-50.%)). During the ECA the populations do not differ in either  
7 size ( $W=41$ ,  $p=0.7$ ) or shape ( $F(5,11)=1.4$ ,  $p=0.3$ ), nor do they differ during the LCA (size:  
8  $X^2=2.2$ ,  $df=4$ ,  $p=0.7$ ; shape:  $F(36,64)=1.2$ ,  $p=0.2$ ). However, specimens attributed to the Early  
9 and Late Ceramic differ in shape ( $F(6,103)=4.2$ ,  $p=0.0008$ ;  $CVP=67.8\%$  (CI=64.5-71.9%)) but  
10 not in size ( $W=1317$ ,  $p=0.3$ ).

11 Similarly to the ones from Grande-Terre, Basse-Terre populations differ in shape  
12 ( $F(115,240)=1.4$ ,  $p=0.02$ ;  $CVP=22.8\%$  (CI:12.3-33.5%)), but not in size ( $X^2=4.9$ ,  $df=5$ ,  $p=0.4$ ).

13 Finally and again similarly, in Marie-Galante, the populations do not differ in size ( $X^2=6.2$ ,  
14  $df=9$ ,  $p=0.7$ ) but differ in shape ( $F(66,816)=2.03$ ,  $p=6.1e-06$ );  $CVA=24.6\%$  (CI:16.1-33.9);  
15 SI.5.1-2). Specimens attributed to the Early and Late Ceramic differ in shape ( $F(12,143)=3.31$ ,  
16  $p=0.0003$ ;  $CVP=63\%$  (CI:59.5-66.3%)), but not in size ( $W=2646$ ,  $p=0.2$ ). We detect no  
17 differences between the ECA and ECB (size:  $X^2=1.1$ ,  $df=1$ ,  $p=0.29$ ; shape:  $F(16,66)=1.1$ ,  
18  $p=0.4$ ) whereas specimens differ in shape between the LCA and LCB ( $F(2,70)=5.5$ ,  $p=0.006$ ;  
19  $CVP=65.1\%$  (CI=50-81.3%)), but not size ( $W=323$ ,  $p=0.3$ ; SI.5.1-2).

20

## 21 **5. DISCUSSION**

22 Three morphometric clusters, corresponding to three biogeographic units, were identified  
23 from the molar size and shape variation: one in Martinique in the south, one in the center islands  
24 of the archipelago (Barbuda, Antigua, Guadeloupe, and Marie-Galante), and one in the  
25 Northern islands (including Saint-Martin, Saba, Saint-Eustatius, Saint-Kitts, and Nevis).

1 Morphological distances between island cannot be explained by the geographic distances  
2 between them since some geographically close islands are distant morphometrically (e.g.  
3 Antigua (central cluster) is 83 km far from Nevis (northern cluster), and 106 km far from Basse-  
4 Terre (central cluster)).

5 This geographic variation greatly outweighs temporal variation, with only slight differences  
6 in molar morphology linked to cultural time periods within each geographical cluster. Our  
7 results thus support long term biogeographic patterning of morphological variation over the  
8 span of ca. 2,000 years.

9

### 10 ***5.1 Morphological diversity and rice rat taxonomy***

11 By only working on the first lower molars only a small portion of the entire phenotype of  
12 the organism is quantified. However, teeth are the most abundant rodents remains in  
13 archeological or paleontological sites, and they are widely used to infer the systematic,  
14 taxonomy and spatio-temporal patterns in this group (e.g. Hulme-Beaman et al., 2018a; Stoetzel  
15 et al., 2017). Tooth morphology is the result of both an adaptive and an heritability component  
16 (Bader, 1965; Polly and Mock, 2018; Renaud et al., 2006). Given the absence of genetic and  
17 morphometric data on exactly the same specimens, which make it impossible to draw definitive  
18 conclusions on the taxonomy of rice rats, the strong biogeographic patterning observed in tooth  
19 morphology could nonetheless be used to infer the diversity of Antillean rice rats and discuss  
20 taxonomical attributions. Our results reveal three distinct morphotypes likely corresponding to  
21 the three genera previously described in earlier morphometric and ancient DNA research (Brace  
22 et al., 2015; Turvey et al., 2010). The Martinican archaeological specimens (89 specimens)  
23 likely correspond to *Megalomys desmarestii* (Fischer, 1829), the only species described from  
24 the island (Friant, 1941; Trouessart, 1885) and for which only four specimens have been  
25 molecularly analyzed (Brace et al., 2015). *Megalomys luciae* (Forsyth Major, 1901) specimens

1 from Sainte-Lucia were not included in this study. However, specimens from Barbuda, where  
2 *Megalomys audreyae* was previously described (Hopwood, 1926), were found to be  
3 morphologically closer to specimens from the central islands, including Grande-Terre and  
4 Antigua, where *Antillomys rayi* was genetically identified (Brace et al., 2015). The slight  
5 morphometric differences revealed by our analyses (407 specimens) between the central islands  
6 may correspond to intra-specific variation within *Antillomys rayi* although the possibility that  
7 our sample includes several distinct species (with morphometrically closely similar first lower  
8 molars) could not be excluded. Finally, the third cluster including specimens from the Northern  
9 islands (644 specimens) likely corresponds to *Pennatomys*, with *Pennatomys nivalis* described  
10 from the Saint-Kitts Bank (Turvey et al., 2010). Brace et al. (2015), based on the Cytochrome  
11 b mitochondrial gene, observed some genetic differentiation between islands across the Saint-  
12 Kitts Bank, with 2% of genetic divergence between specimens from Nevis and Saint-Kitts, and  
13 5-7% divergence between these specimens and those from Saint-Eustatius. These molecular  
14 analyses are in perfect agreement with our morphometrical data (specimens from Nevis and  
15 Saint-Kitts being morphological closer than those from Saint-Eustatius) and suggest  
16 intraspecific or inter-specific variation. Our results suggest that the two geographically-distant  
17 island groupings, Martinique in the South and the Northern islands, are phenotypically more  
18 similar to each other, than to those of the geographical closer central islands. This is consistent  
19 with molecular data showing a sister relationship between *Megalomys* and *Pennatomys*, while  
20 *Antillomys* is more distantly related (Brace et al., 2015). Further research on this insular group  
21 taxonomy should seek to combine morphometric analysis with ancient DNA of the same  
22 specimens, in order to confirm the taxonomy of all investigated populations.

23

## 24 ***5.2 Influence of ecological factors within clusters***

1 Rice rats from the Northern islands had very small molar size compared to the rest of the  
2 archipelago. A similar pattern has been observed in the *Anolis* lizards from Saint-Martin which  
3 particularly small size has been linked to the presence of competition (Brown and Wilson, 1956;  
4 Losos, 2000; Losos and Ricklefs, 2009; Roughgarden, 1995). Accordingly, the size of the  
5 oryzomyines from Saint-Martin and the other northern islands might be caused by the presence  
6 of a competitor species (e.g. *Amblyrhiza inundata* identified in the Anguilla bank during the  
7 Pleistocene; McFarlane et al., 2014) or by the existence of peculiar, but yet to be determined,  
8 local conditions which impacted species size on these islands.

9 In the present study comparison between chrono-cultural periods was greatly limited by the  
10 number of archaeological sites available for each island and period. Despite these limitations,  
11 we detected some differences in shape, but not in size, between diachronic populations, more  
12 especially between the Early and Late Ceramic in Martinique, Marie-Galante, and Guadeloupe  
13 Grande-Terre. Diachronic differentiation between archaeological rodent populations have been  
14 identified, in other species, using a similar methodology (e.g. Cucchi et al., 2014; Hulme-  
15 Beaman et al., 2018b) and has been interpreted as the result of a variety of causes including  
16 human landscape modification, climatic change, or a combination of both causes.

17 In the case of oryzomyine, their past and current distribution ranges on the South American  
18 continent indicates that climatic change has affected their distribution (Vázquez-Domínguez et  
19 al., 2020; Vickery et al., 2016). In the Lesser Antilles archipelago, a climatic change is  
20 registered around 900-1000 CE, and coincide to the transition between the Early and Late  
21 Ceramic Age. This change is linked with a transformation from a wet to a dryer and stormier  
22 climate across the archipelago (Beets et al., 2006; Bertran et al., 2004). In between these two  
23 periods, Pre-Columbian populations also experienced societal changes, identifiable in material  
24 culture and habitat (Fitzpatrick, 2015; Hofman et al., 2007; Siegel et al., 2015) and



1 bioarchaeological studies point to a transformation in the management and consumption of  
2 resources (Grouard, 2004, 2007, 2010; Wing, 2001a).

3 If these elements are to be considered, further investigations are required to define the  
4 impact of ecological factors on insular rice rat morphology, which is particularly challenging  
5 when dealing with extinct taxa.

6

### 7 ***5.3 No strong evidence for human-mediated dispersal***

8 A proposed northward river-based connection between the Amazon basin and the Caribbean  
9 sea during the late Miocene (Wilkinson et al., 2010) may have facilitated broadly simultaneous  
10 overwater dispersal of many South American mainland vertebrates to the Lesser Antilles  
11 (review in Brace et al., 2015). For instance, the genus *Leptodactylus* (Anura, Leptodactylidae)  
12 is considered to have colonized the Lesser Antilles by dispersal across water in the mid-  
13 Cenozoic (Camargo, Heyer, & de Sá, 2009; Hedges & Heinicke, 2007). According to genetic  
14 data the multiple colonization events of oryzomyine in the archipelago date to the same period  
15 (late Miocene) (Brace et al., 2015), despite their absence in the paleontological records  
16 (Grouard, 2015). Our results show only slight phenotypic changes through archaeological  
17 chrono-cultural periods, between 500 BCE and 1500 CE, as well as the continuous presence of  
18 three clearly defined geographic clusters supporting the hypothesis of an ancient arrival of the  
19 group in the archipelago.

20 Prior to their extinction, the rice rats of the Lesser Antilles lived close to human settlements  
21 and crop areas (Allen, 1942; Pinchon, 1967; Trouessart, 1885; Wing, 2001b). This tendency to  
22 commensalism was probably established since the first human occupation in the archipelago.  
23 Indeed, zooarchaeological studies highlight their importance in the subsistence economy of  
24 local human population throughout the entire Ceramic Age (Grouard, 2004, 2010; Wing,  
25 2001b) and thus long-term interactions between these rodents and the Pre-Columbian

1 populations. On the other hand, in the north of the archipelago the morphometric variation is  
2 well structured per island, a pattern that favor a hypothesis of no (or at least not strong) inflow  
3 from external rice rats populations that would have disrupted or smoothed out the inter-island  
4 phenotypic structure. In the center, the differences between island phenotypes is less structured,  
5 and the possibility of inter-island connections cannot be completely excluded. However, study  
6 of additional specimens and archaeological sites would be necessary to confirm these  
7 hypotheses. As the prevailing morphometric variation is geographically structured through time  
8 we suggest an absence of long-distance connection between islands from the different clusters,  
9 and thus an absence of human transport of oryzomyines from one island to another.

10 Moreover, rice rats fail to meet five of the 10 criteria proposed for classifying species as  
11 impacted by humanly-mediated translocations (Giovas, 2019; Heinsohn, 2003, 2010), and two  
12 of them could not be applied to this study. Even though the presence of oryzomyines is lacking  
13 in the paleontological and archaeological faunal records (criteria 2) prior to the Ceramic Age  
14 where they abruptly appear (criteria 3) (Grouard, 2015), they likely colonized the Lesser  
15 Antilles during the late Miocene (Brace et al., 2015). Rice rats show commensal tendency  
16 (criterion 5) on the continent (Guilday, 1972; Guilday and Parmalee, 1965; Vickery et al., 2016)  
17 and are found in zooarchaeological contexts in association with a plethora of naturally dispersed  
18 species (criterion 8) consumed by humans (Grouard, 2004, 2010; Newsom and Wing, 2004;  
19 Wing, 2001b), as well as with the agouti, another rodent potentially introduced (Allen, 1942;  
20 Newsom and Wing, 2004) and managed (Govoni and Fielding, 2001; Hardouin, 1995)  
21 (criterion 7). At the scale of the archipelago, their distribution is wide (criterion 4), their  
22 phenotypic and molecular differentiation is geographically cohesive (criterion 1) and inter-  
23 island differences persist through time (criterion 6, applied here to morphometric data). Finally,  
24 the criteria based on comparisons with historically documented species introduction (criterion  
25 9) and diachronic reconstruction of invasion frontiers (criterion 10) cannot be applied due to

1 data limitation. Overall, the evidence from previous analyses alongside our current research  
2 favors a non-anthropogenic dispersion of the group into the archipelago, or if contacts have existed,  
3 newly human-introduced populations from one island to another have not persisted and were  
4 not detected.

5

## 6 **6. CONCLUSIONS**

7 This study significantly contributes to our knowledge and understanding of the past  
8 diversity of the tribe Oryzomyini in the Lesser Antilles archipelago. Over a thousand specimens  
9 of these now extinct taxa were analyzed using geometric morphometrics, allowing the first  
10 exploration of their archaeobiogeography. The rice rats show diverse but very homogenous  
11 molar morphotypes defined by geographic parameters, which remain largely stable for the  
12 2,000 years of the Ceramic Age in the Lesser Antilles archipelago. The persistence of this strong  
13 archaeobiogeographical phenotypic pattern throughout the Ceramic Age supports a scenario of  
14 a pre-human dispersal of Oryzomyini species. While rice rats were a component of human diet  
15 throughout the Ceramic Age, our overall results do not support an initial hypothesis of human-  
16 mediated transport of rice rats between and within the three geographic entities, despite the  
17 evidences of transportation of cultivated plants, domesticated animals and raw materials.  
18 Additional studies combining geometric morphometric and ancient DNA analyses on the exact  
19 same specimens would allow for the consolidation of the archaeobiogeography, taxonomy and  
20 systematics of these extinct endemic rodents, and better identify the environmental adaptations  
21 that might have driven the establishment of rice rat populations across the archipelago.

22

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10

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19

20 **Author contributions:**

21 Author contributions: AE and SG conceived the ideas; DB, KD, SG, SP and GR conducted  
22 the fieldwork and collected the material, KD and SG identified the archaeological bones; MD  
23 acquired the data; MD and AE performed the analyses; MD, AE, SG, VN, interpreted the results  
24 and MD led the writing with assistance from AE, SG and VN.

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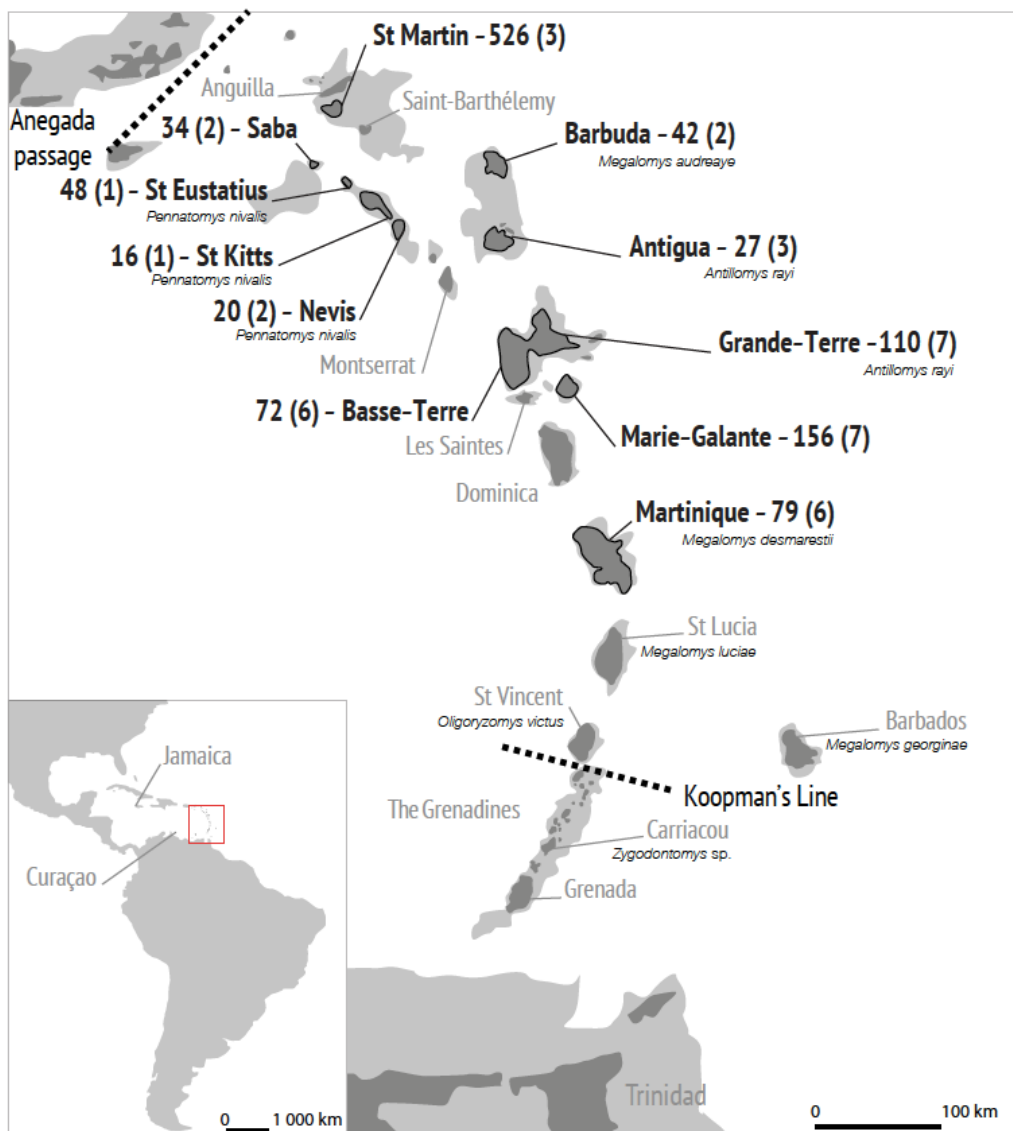
1 **Table legend:**

2 **Table 1** - Number of archaeological rice rat lower first molars studied, organized by chrono-cultural period,  
3 archaeological site and island of origin.

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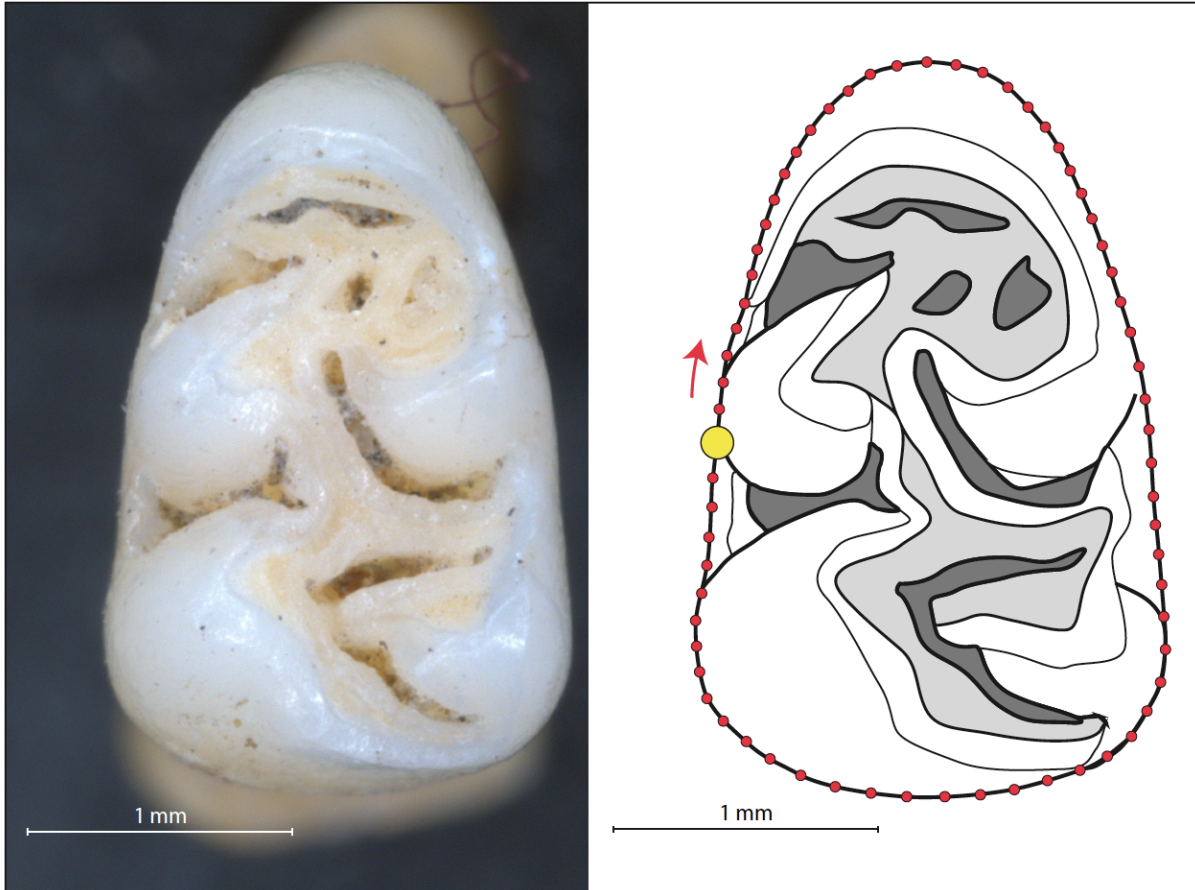
5 **Figures legends:**

6 **Figure 1** - Map of the Lesser Antilles archipelago. The seven islands investigated are highlighted and followed by  
7 the number of archaeological rice rats (tribe Oryzomyini) teeth analyzed. The number of archaeological sites  
8 studied are in brackets. Information about the sites can be found in Table 1. Grey shadows indicate the geological  
9 banks exposed during the Pleistocene (Hedges, 2001; McPhee and Flemming, 1999; Pregill et al., 1994). Dashed  
10 lines in the North mark the Anegada passage (Jany et al., 1990) and in the South Koopman's Line (Genoways et  
11 al., 2010).



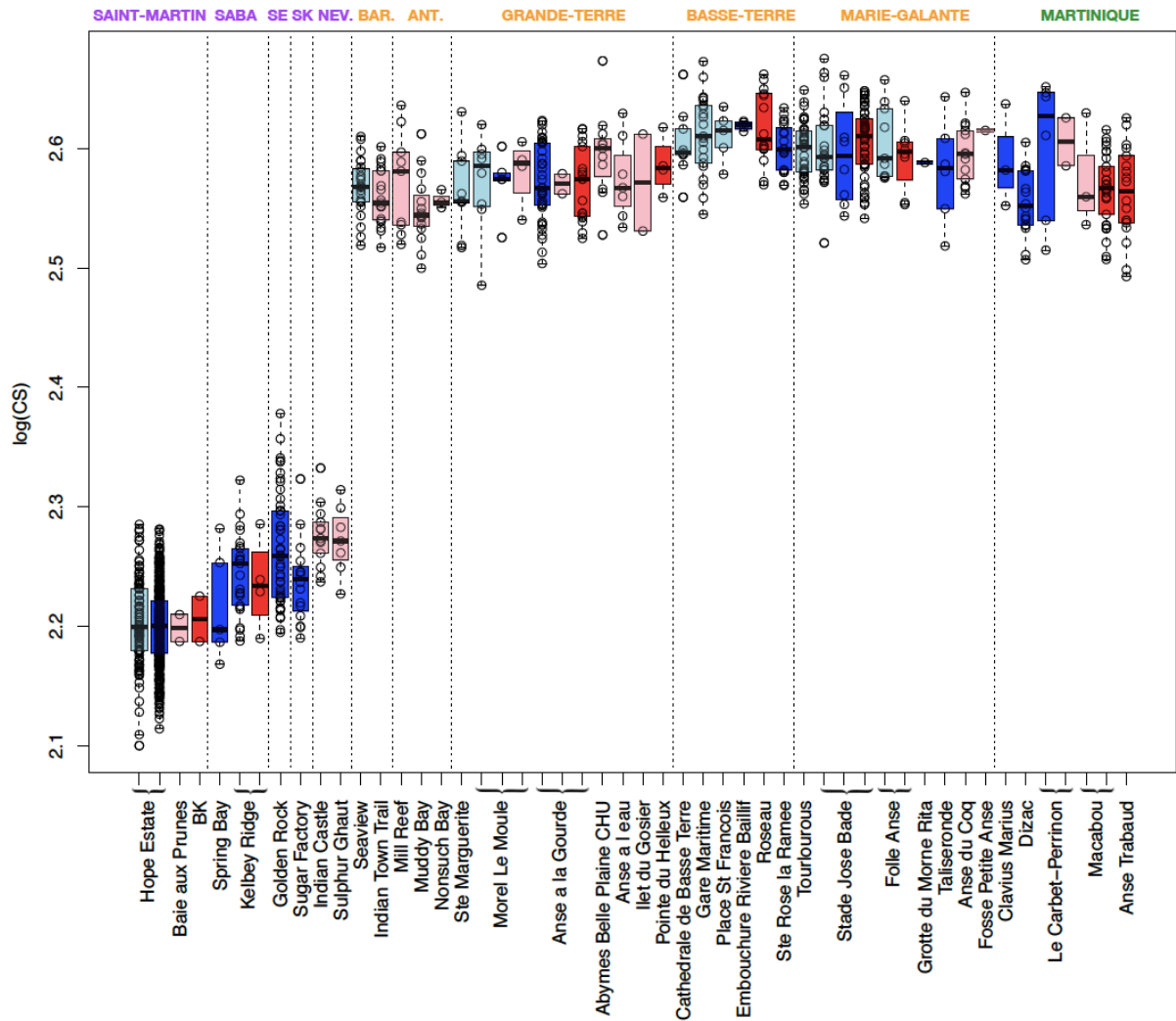
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1 **Figure 2** - Left: Occlusal view of a first lower molar of a Lesser Antillean rice rat (specimen SRA-Guadeloupe-  
2 HE-089-D from Hope Estate, Saint-Martin). Right: Geometric morphometric protocol including one landmark  
3 (large yellow dot) and 65 sliding semi-landmarks along the outside curvature of the tooth, recorded in a clockwise  
4 direction.



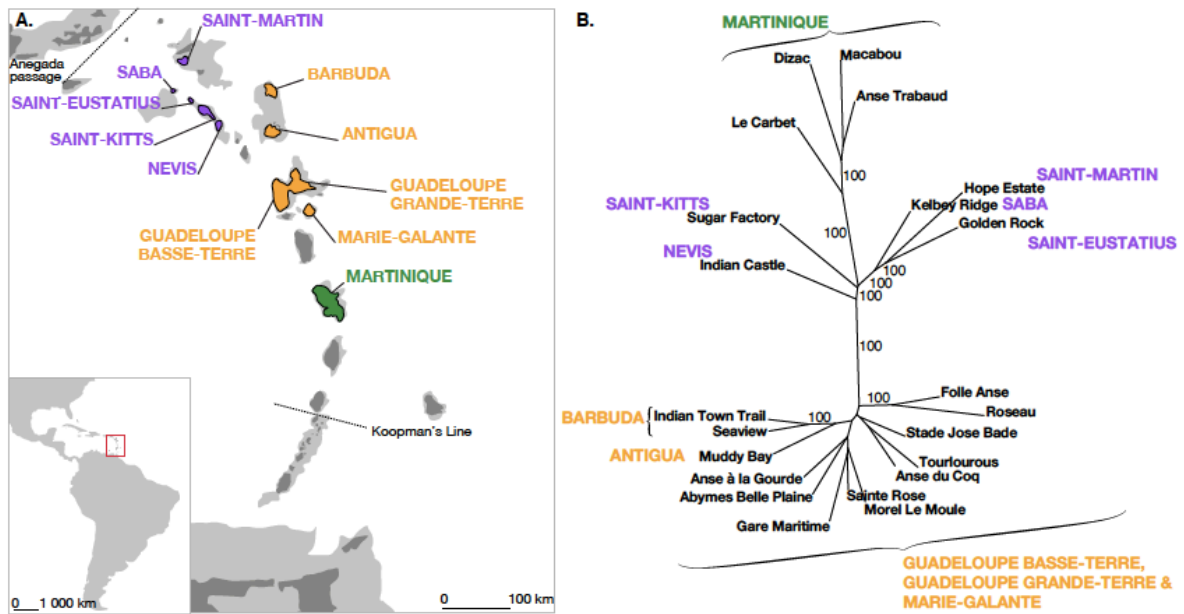
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1 **Figure 3** - Size variation between rice rat populations of the Lesser Antilles. Boxplots of the log-transformed  
 2 centroid size of the lower M1. Specimens were grouped by island, site and chronological occupation phase. In  
 3 light blue: Early Ceramic Age A, dark blue: Early Ceramic Age B, pink: Late Ceramic Age A, red: Late Ceramic  
 4 Age B. SE: Saint-Eustatius, SK: Saint-Kitts, NEV.: Nevis, ANT.: Antigua, BAR.: Barbuda. The islands names are  
 5 colored according to the three shape clusters identified (Fig. 4) (purple: Northern islands, yellow: Central islands,  
 6 green: Southern island).

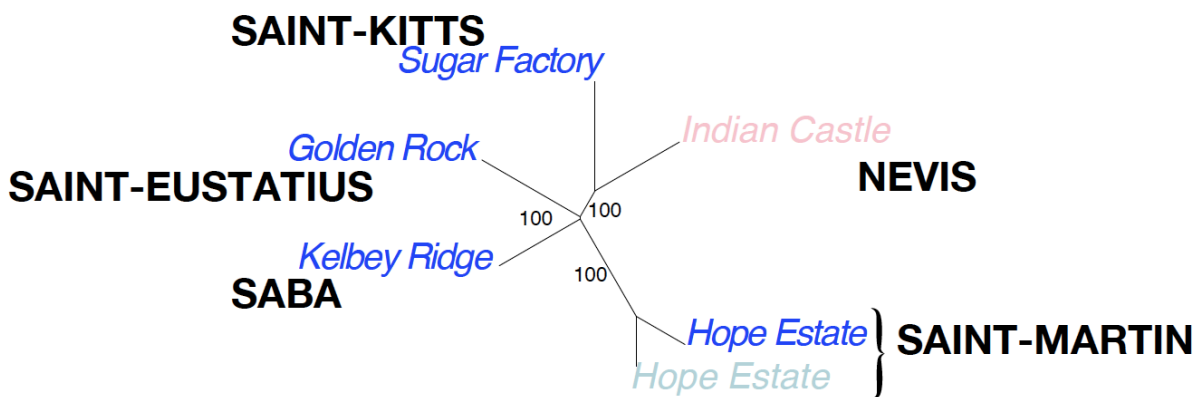


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1 **Figure 4 - A. Phenotypic relationship between sites across the Lesser Antilles.** Mean branch lengths neighbor-  
 2 joining network of the bootstrapped Mahalanobis distances (1000 replicates) with mention of the bootstrap  
 3 percentages above 50%. Only sites with more than 10 specimens were included. Island names are colored by their  
 4 geographic and morphometrical cluster attribution (purple: Northern islands, yellow: Central islands, green:  
 5 Southern islands). **B. Map of the studied islands** colored by the three shape clusters identified.

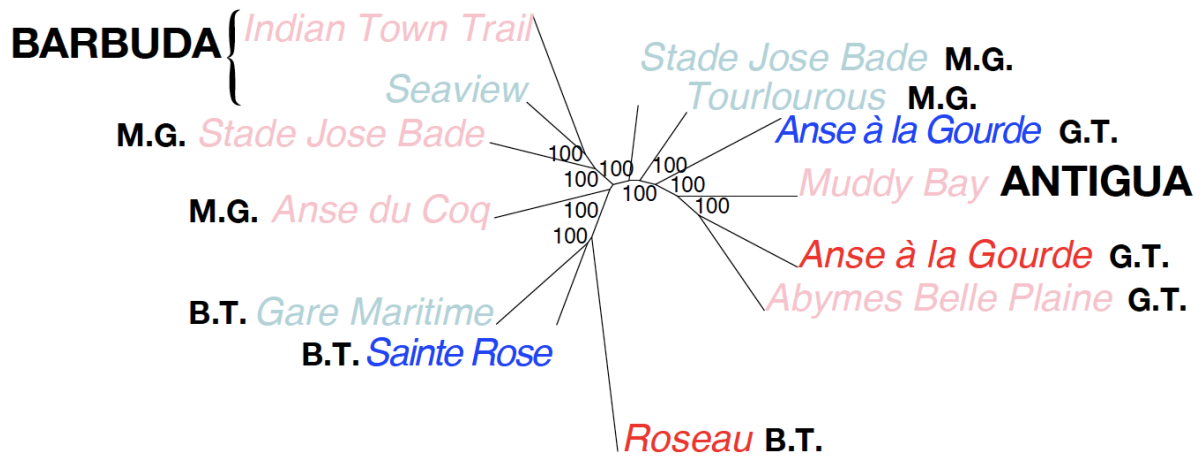


6  
 7 **Figure 5 - Phenotypic relationship between sites of the Northern islands.** Mean branch lengths neighbor-  
 8 joining network of the bootstrapped Mahalanobis distances (1000 replicates) with mention of the bootstrap  
 9 percentages above 50%. Site names are colored by chronological occupation phases (light blue: Early Ceramic A,  
 10 dark blue: Early Ceramic B, pink: Late Ceramic A, red: Late Ceramic B). Only sites with more than 10 specimens  
 11 were included.



12  
 13

1 **Figure 6 - Phenotypic relationship between sites of the Central islands.** Mean branch lengths neighbor-joining  
 2 network of the bootstrapped Mahalanobis distances (1000 replicates) with mention of the bootstrap percentages  
 3 above 50%. Site names are colored by chronological occupation phases (light blue: Early Ceramic A, dark blue:  
 4 Early Ceramic B, pink: Late Ceramic A, red: Late Ceramic B). M.G.: Marie-Galante, B.T.: Guadeloupe Basse-  
 5 Terre, GT: Guadeloupe Grande-Terre. Only sites with more than 10 specimens were included.



6