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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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21

22

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

3

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 4th 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 19th 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 (M₁, 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 M₁ 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>

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).

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

11 **REFERENCES**

12 Adams DC, Collyer ML and Kaliontzopoulou A (2018) Geomorph: Software for geometric
13 morphometric analyses. R package version 3.0.1. [https://cran.r-](https://cran.r-project.org/package=geomorph)
14 [project.org/package=geomorph](https://cran.r-project.org/package=geomorph).

15 Albrecht GH (1980) Multivariate analysis and the study of form, with special reference to
16 canonical variate analysis. *American Zoologist* 20(4): 679–693.

17 Allen GM (1942) *Extinct and Vanishing mammals of the Western Hemisphere*. Lancaster,
18 Pennsylvania: The Intelligencer Princtor Co.

19 Bader RS (1965) Heritability of dental characters in the house mouse. *Evolution*. JSTOR 378–
20 384.

21 Baker R and Genoways H (1978) Zoogeography of Antillean Bats. *Mammalogy Papers:*
22 *University of Nebraska State Museum*.

23 Barbotin PM (1970) Les sites archéologiques de Marie-Galante (Guadeloupe). *Proceedings of*
24 *the Third International Congress for the Study of Pre-Columbian Cultures of the Lesser Antilles*
25 27–44.

1 Baylac M and Friess M (2005) Fourier descriptors, Procrustes superimposition, and data
2 dimensionality: an example of cranial shape analysis in modern human populations. *Modern*
3 *morphometrics in physical anthropology* 145–165.

4 Beets CJ, Troelstra SR, Grootes PM, Nadeau M-J, Borg K v, de Jong AF, et al. (2006) Climate
5 and pre-Columbian settlement at Anse à la Gourde, Guadeloupe, Northeastern Caribbean.
6 *Geoarchaeology* 21(3): 271–280.

7 Benjamini Y and Hochberg Y (1995) Controlling the false discovery rate: a practical and
8 powerful approach to multiple testing. *Journal of the royal statistical society. Series B*
9 *(Methodological)* 289–300.

10 Bérard B (2012) Pre-Columbian Antillean civilizations in an archipelagic perspective. paper
11 presented at the 1st Garifuna International Conference. Available at: [https://hal.univ-](https://hal.univ-antilles.fr/hal-00961357/document)
12 [antilles.fr/hal-00961357/document](https://hal.univ-antilles.fr/hal-00961357/document).

13 Bertran P, Bonnissent D, Imbert D, Lozouet P, Serrand N and Stouvenot C (2004) Paléoclimat
14 des Petites Antilles depuis 4000 ans BP : l'enregistrement de la lagune de Grand-Case à Saint-
15 Martin. *Comptes Rendus Geoscience* 336(16): 1501–1510: doi:10.1016/j.crte.2004.09.009.

16 Bond J (1999) *A Field Guide to the Birds of the West Indies*. Houghton Mifflin Harcourt.

17 Bonnissent D (2008) Archéologie précolombienne de l'île de Saint-Martin, Petites Antilles
18 (3300 BC-1600 AD). PhD Thesis, Université de Provence-Aix-Marseille I.

19 Bonnissent D, Serrand N, Bruxelles L, Fouéré P, Grouard S, Sellier-Ségard N, et al. (2014)
20 Archéoécologie des sociétés insulaires des Petites Antilles au Mésoindien: l'enjeu des
21 ressources à Saint-Martin. *Séance de la Société préhistorique française de Rennes*, 213–260.

22 Bonnissent (Dir.) D (2013) *Les gisements précolombiens de la Baie Orientale: campements du*
23 *Mésoindien et du Néoindien sur l'île de Saint-Martin (Petites Antilles)*. Éditions de la Maison
24 des sciences de l'homme.

1 Boudadi-Maligne M, Bailon S, Bochaton C, Casagrande F, Grouard S, Serrand N, et al. (2016)
2 Evidence for historical human-induced extinctions of vertebrate species on La Désirade (French
3 West Indies). *Quaternary Research* 85(1): 54–65.

4 Brace S, Turvey ST, Weksler M, Hoogland ML and Barnes I (2015) Unexpected evolutionary
5 diversity in a recently extinct Caribbean mammal radiation. *Proceedings Royal Society*
6 *publishing B* 282: 9.

7 Brown WL and Wilson EO (1956) Character displacement. *Systematic zoology* 5(2): 49–64.

8 Camargo A, Heyer WR and de Sá RO (2009) Phylogeography of the frog *Leptodactylus validus*
9 (Amphibia: Anura): patterns and timing of colonization events in the Lesser Antilles. *Molecular*
10 *Phylogenetics and Evolution* 53(2): 571–579.

11 Crock JG and Petersen JB (2004) Inter-island exchange, settlement hierarchy, and a Taino-
12 related chiefdom on the Anguilla Bank, Northern Lesser Antilles. *Late Ceramic Age Societies*
13 *in the Eastern Caribbean*. Eric Taladoire, 139–158.

14 Cucchi T (2009) Le commensalisme de la souris et les sociétés néolithiques méditerranéennes.
15 Collège de France.

16 Cucchi T, Barnett R, Martínková N, Renaud S, Renvoisé E, Evin A, et al. (2014) The changing
17 pace of insular life: 5000 years of microevolution in the Orkney vole (*Microtus arvalis*
18 *orcadensis*). *Evolution* 68(10): 2804–2820.

19 Darviche D and Orsini P (1982) Critères de différenciation morphologique et biométrique de
20 deux espèces de souris sympatriques: *Mus spretus* et *Mus musculus domesticus*. *Mammalia*
21 46(2): 205–218.

22 Darviche D, Orth A and Michaux J (2006) *Mus spretus* et *M. musculus* (Rodentia, Mammalia)
23 en zone méditerranéenne: différenciation biométrique et morphologique: application à des
24 fossiles marocains pléistocènes/*Mus spretus* and *M. musculus* (Rodentia, Mammalia) in the

1 Mediterranean zone: biometric and morphological differentiation: application to Pleistocene
2 Moroccan fossils. *Mammalia* 70(1–2): 90–97.

3 Dobigny G, Baylac M and Denys C (2002) Geometric morphometrics, neural networks and
4 diagnosis of sibling *Taterillus* species (Rodentia, Gerbillinae). *Biological Journal of the*
5 *Linnean Society*. Oxford University Press 77(3): 319–327.

6 Evin A, Cucchi T, Cardini A, Vidarsdottir US, Larson G and Dobney K (2013) The long and
7 winding road: identifying pig domestication through molar size and shape. *Journal of*
8 *Archaeological Science* 40(1): 735–743.

9 Fabre P-H, Pagès M, Musser GG, Fitriana YS, Fjelds\aa J, Jennings A, et al. (2013) A new
10 genus of rodent from Wallacea (Rodentia: Muridae: Murinae: Rattini), and its implication for
11 biogeography and Indo-Pacific Rattini systematics. *Zoological Journal of the Linnean Society*.
12 Oxford University Press 169(2): 408–447.

13 Fischer JB (1829) *Synopsis Mammalium*. Stuttgart.

14 Fitzpatrick SM (2015) The pre-Columbian Caribbean: Colonization, population dispersal, and
15 island adaptations. *PaleoAmerica* 1(4): 305–331.

16 `Forsyth Major CI (1901) The musk-rat of Santa Lucia (Antilles). *Annals and Magazine of*
17 *Natural History Series* 7(7): 204–206.

18 Friant M (1941) Notes anatomiques sur les *Megalomys* des Antilles. *Bulletin de la Société*
19 *zoologique de France* 66: 122–129.

20 Friesen VL, Smith AL, Gomez-Diaz E, Bolton M, Furness RW, González-Solís J, et al. (2007)
21 Sympatric speciation by allochryony in a seabird. *Proceedings of the National Academy of*
22 *Sciences* 104(47): 18589–18594.

23 Genoways HH, Kwiecinski GG, Larsen PA, Pedersen SC, Larsen RJ, Hoffman JD, et al. (2010)
24 Bats of the Grenadine Islands, West Indies, and placement of Koopman’s line. *Chiroptera*
25 *Neotropical* 16(1): 529–549.

1 Giovas CM (2018) Pre-Columbian Amerindian Lifeways at the Sabazan Site, Carriacou, West
2 Indies. *The Journal of Island and Coastal Archaeology* 13(2): 161–190.

3 Giovas CM (2019) The beasts at large—perennial questions and new paradigms for Caribbean
4 translocation research. Part I: Ethnozoogeography of mammals. *Environmental Archaeology*
5 24(2): 182–198.

6 Giovas CM, Kamenov GD, Fitzpatrick SM and Krigbaum J (2016) Sr and Pb isotopic
7 investigation of mammal introductions: Pre-Columbian zoogeographic records from the Lesser
8 Antilles, West Indies. *Journal of Archaeological Science* 69: 39–53.

9 Giovas CM, LeFebvre MJ and Fitzpatrick SM (2012) New records for prehistoric introduction
10 of Neotropical mammals to the West Indies: evidence from Carriacou, Lesser Antilles. *Journal*
11 *of Biogeography* 39(3): 476–487.

12 Gittins R (1985) Canonical variate analysis. *Canonical Analysis*. Springer, 67–95.

13 Goodall CR (1995) Procrustes methods in the statistical analysis of shape revisited. *Current*
14 *issues in statistical shape analysis* 18–33.

15 Govoni G and Fielding D (2001) Paca (*Agouti paca*) and Agouti (*Dasyprocta* spp.)—
16 Minilivestock Production in the Amazonas State of Venezuela. *Tropicultura* 19: 56–60.

17 Grouard S (2001) Subsistance, systèmes techniques et gestion territoriale en milieu insulaire
18 antillais précolombien: exploitation des vertébrés et des crustacés aux époques Saladoïdes et
19 Troumassoïdes de Guadeloupe (400 av. JC à 1500 ap. JC). Paris 10.

20 Grouard S (2004) Variation des stratégies de subsistance des Précolombiens à Hope Estate,
21 Saint-Martin (Petites Antilles), d’après l’analyse des restes des petits vertébrés. *Petits Animaux*
22 *et Sociétés Humaines. Du Complément Alimentaire aux Ressources Utilitaires* 441–467.

23 Grouard S (2007) Modes de vie des Précolombiens des Antilles françaises. Synthèse des
24 données archéozoologiques. *Les nouvelles de l’archéologie* (108/109): 91–101.

- 1 Grouard S (2010) Caribbean archaeozoology. *Current Advances in Latin-American*
2 *Archaeozoology. International Council for Archaeozoology: Universidad de Buenos Aires,*
3 *Mexico* 89–109.
- 4 Grouard S (2015) Peuplemens humains et animaux de la Caraïbe depuis 10 000 ans. HDR,
5 Université de Provence-Aix-Marseille I.
- 6 Guilday JE (1972) Archaeological Evidence of *Scalopus aquaticus* in the Upper Ohio Valley.
7 *Journal of Mammalogy* 53(4): 905–907.
- 8 Guilday JE and Parmalee PW (1965) Animal remains from the Sheep Rock Shelter (36Hu1),
9 Huntingdon County, Pennsylvania. *Pennsylvania Archaeologist* 35(1): 34–49.
- 10 Hardouin J (1995) Minilivestock: from gathering to controlled production. *Biodiversity &*
11 *Conservation*. Springer 4(3): 220–232.
- 12 Hedges SB (1999) Distribution patterns of amphibians in the West Indies. *Patterns of*
13 *distribution of amphibians: a global perspective* 211–254.
- 14 Hedges SB (2001) Biogeography of the West Indies: an overview. *Biogeography of the West*
15 *Indies: patterns and perspectives* 15–33.
- 16 Hedges SB and Heinicke MP (2007) Molecular phylogeny and biogeography of West Indian
17 frogs of the genus *Leptodactylus* (Anura, Leptodactylidae). *Molecular Phylogenetics and*
18 *Evolution* 44(1): 308–314.
- 19 Heinsohn TE (2003) Animal translocation: long-term human influences on the vertebrate
20 zoogeography of Australasia (natural dispersal versus ethnophoresy). *Australian Zoologist*
21 32(3): 351–376.
- 22 Heinsohn TE (2010) Marsupials as introduced species: Long-term anthropogenic expansion of
23 the marsupial frontier and its implications for zoogeographic interpretation. *Altered ecologies:*
24 *Fire, climate and human influence on terrestrial landscapes* 133–176.

1 Henderson RW (1992) Consequences of predator introductions and habitat destruction on
2 amphibians and reptiles in the post-Columbus West Indies. *Caribbean journal of science* 28(1–
3 2): 1–10.

4 Hofman CL, Bright AJ, Boomert A and Knippenberg S (2007) Island rhythms: the web of social
5 relationships and interaction networks in the Lesser Antillean archipelago between 400 BC and
6 AD 1492. *Latin American Antiquity* 18(3): 243–268.

7 Hofman CL, Bright AJ and Hoogland ML (2006) Archipelagic resource procurement and
8 mobility in the northern Lesser Antilles: the view from a 3000-year-old tropical forest campsite
9 on Saba. *Journal of Island & Coastal Archaeology* 1(2): 145–164.

10 Hofman CL, Bright AJ, Hoogland ML and Keegan WF (2008) Attractive ideas, desirable
11 goods: examining the Late Ceramic Age relationships between Greater and Lesser Antillean
12 societies. *The Journal of Island and Coastal Archaeology* 3(1): 17–34.

13 Hofman CL and Hoogland ML (2011) Unravelling the multi-scale networks of mobility and
14 exchange in the pre-colonial circum-Caribbean. *Communities in contact: Essays in*
15 *archaeology, ethnohistory and ethnography of the Amerindian Circum-Caribbean* 14–44.

16 Hopwood AT (1926) XLVI.—A fossil rice-rat from the Pleistocene of Barbuda. *Journal of*
17 *Natural History* 17(99): 328–330.

18 Horst GR, Hoagland DB and Kilpatrick CW (2001) The mongoose in the West Indies: the
19 biogeography and population biology of an introduced species. *Biogeography of the West*
20 *Indies*. CRC Press, 435–450

21 Hulme-Beaman A, Claude J, Chaval Y, Evin A, Morand S, Vigne JD, et al. (2018a) Dental
22 Shape Variation and Phylogenetic Signal in the Rattini Tribe Species of Mainland Southeast
23 Asia. *Journal of Mammalian Evolution* 1–12.

1 Hulme-Beaman A, Cucchi T, Evin A, Searle JB and Dobney K (2018b) Exploring *Rattus*
2 *praetor* (Rodentia, Muridae) as a possible species complex using geometric morphometrics on
3 dental morphology. *Mammalian Biology* 92: 62–67.

4 Jansa SA, Barker FK and Heaney LR (2006) The pattern and timing of diversification of
5 Philippine endemic rodents: evidence from mitochondrial and nuclear gene sequences.
6 *Systematic Biology*. Oxford University Press 55(1): 73–88.

7 Jany I, Scanlon KM and Mauffret A (1990) Geological interpretation of combined Seabeam,
8 Gloria and seismic data from Anegada Passage (Virgin Islands, north Caribbean). *Marine*
9 *Geophysical Researches* 12(3): 173–196.

10 Kadmon R and Allouche O (2007) Integrating the effects of area, isolation, and habitat
11 heterogeneity on species diversity: a unification of island biogeography and niche theory. *The*
12 *American Naturalist* 170(3): 443–454.

13 Kimura BK, LeFebvre MJ, deFrance SD, Knodel HI, Turner MS, Fitzsimmons NS, et al. (2016)
14 Origin of pre-Columbian guinea pigs from Caribbean archeological sites revealed through
15 genetic analysis. *Journal of Archaeological Science: Reports* 5: 442–452:
16 doi:10.1016/j.jasrep.2015.12.012.

17 Knippenberg S (2007) *Stone artefact production and exchange among the Lesser Antilles*.
18 Amsterdam University Press.

19 Laffoon JE, Hoogland ML, Davies GR and Hofman CL (2016) Human dietary assessment in
20 the Pre-colonial Lesser Antilles: New stable isotope evidence from Lavoutte, Saint Lucia.
21 *Journal of Archaeological Science: Reports* 5: 168–180.

22 Laffoon JE, Plomp E, Davies GR, Hoogland ML and Hofman CL (2015) The movement and
23 exchange of dogs in the prehistoric Caribbean: An isotopic investigation. *International Journal*
24 *of Osteoarchaeology* 25(4): 454–465.

1 Laffoon JE, Rojas RV and Hofman CL (2013) Oxygen and carbon isotope analysis of human
2 dental enamel from the Caribbean: implications for investigating individual origins.
3 *Archaeometry* 55(4): 742–765.

4 LeFebvre MJ and deFrance SD (2014) Guinea Pigs in the Pre-Columbian West Indies. *The*
5 *Journal of Island and Coastal Archaeology* 9(1): 16–44: doi:10.1080/15564894.2013.861545.

6 LeFebvre MJ, DuChemin G, deFrance SD, Keegan WF and Walczesky K (2019) Bahamian
7 hutia (*Geocapromys ingrahami*) in the Lucayan Realm: pre-Columbian exploitation and
8 translocation. *Environmental Archaeology* 24(2): 115–131.

9 Lord E, Collins C, deFrance S, LeFebvre MJ and Matisoo-Smith E (2018) Complete
10 mitogenomes of ancient Caribbean Guinea pigs (*Cavia porcellus*). *Journal of Archaeological*
11 *Science: Reports* 17: 678–688.

12 Losos JB (2000) Ecological character displacement and the study of adaptation. *Proceedings*
13 *of the National Academy of Sciences*. National Acad Sciences 97(11): 5693–5695.

14 Losos JB and Ricklefs RE (2009) *Adaptation and diversification on islands*. *Nature*. Special
15 Features.

16 Louppe V, Herrel A, Pisanu B, Grouard S and Véron G (2020) Occupancy modelling of two
17 invasive carnivores in two Caribbean islands: implications for insular ecosystems. *Journal of*
18 *Zoology*.

19 Machado LF, Leite YL, Christoff AU and Giugliano LG (2014) Phylogeny and biogeography
20 of tetralophodont rodents of the tribe Oryzomyini (Cricetidae: Sigmodontinae). *Zoologica*
21 *Scripta* 43(2): 119–130.

22 MacPhee RDE and Flemming C (1999) Requiem Aeternam. *Extinctions in near time*. Springer,
23 333–371.

1 Maestri R, Monteiro LR, Fornel R, de Freitas TRO and Patterson BD (2018) Geometric
2 morphometrics meets metacommunity ecology: environment and lineage distribution affects
3 spatial variation in shape. *Ecography* 41(1): 90–100.

4 McFarlane DA, Lundberg J and Maincent G (2014) New specimens of *Amblyrhiza inundata*
5 (Rodentia: Caviomorpha) from the Middle Pleistocene of Saint Barthélemy, French West
6 Indies. *Caribbean Journal of Earth Science* 47: 15–19.

7 McPhee RDE and Flemming C (1999) Requiem aeternam: the last five hundred years of
8 mammalian species extinctions. *Extinctions in near time. Kluwer Academic/Plenum Publishers,*
9 *New York, NY* 333–371.

10 Miljutin A (2010) Notes on the external morphology, ecology, and origin of *Megalomys*
11 *desmarestii* (Sigmodontinae, Cricetidae, Rodentia), The extinct giant rat of Martinique Island,
12 Lesser Antilles. *Estonian Journal of Ecology* 59(3): 216–229.

13 Millien V (2006) Morphological evolution is accelerated among island mammals. *PLoS biology*
14 4(10).

15 Mistretta BA (2019) Grenada’s extinct rice rats (Oryzomyini): Zooarchaeological evidence for
16 taxonomic diversity. *Journal of Archaeological Science: Reports* 24: 71–79.

17 Mol AAA (2006) *Costly Giving, Giving Guaízas: Towards an Organic Model of the Exchange*
18 *of Social Valuables in the Late Ceramic Age Caribbean.* Sidestone Press.

19 Nagorsen DW and Cardini A (2009) Tempo and mode of evolutionary divergence in modern
20 and Holocene Vancouver Island marmots (*Marmota vancouverensis*)(Mammalia, Rodentia).
21 *Journal of Zoological Systematics and Evolutionary Research.* Wiley Online Library 47(3):
22 258–267.

23 Newsom LA and Wing ES (2004) *On land and sea: Native American uses of biological*
24 *resources in the West Indies.* University of Alabama Press.

1 Pagán Jiménez JR, Rodríguez M, Baik LC and Storde YN (2005) La temprana introducción y
2 uso de algunas plantas domésticas, silvestres y cultivos en las Antillas precolombinas. Una
3 primera revaloración desde la perspectiva del ‘arcaico’ de Vieques y Puerto Rico. *Dialogo*
4 *antropológico* 3(10): 7–33.

5 Paradis E and Schliep K (2018) ape 5.0: an environment for modern phylogenetics and
6 evolutionary analyses in R. *Bioinformatics* 1: 3.

7 Pinchon R (Robert) (1967) Quelques aspects de la nature aux Antilles. Available at:
8 <http://agris.fao.org/agris-search/search.do?recordID=US201300591948>.

9 Polly PD and Mock OB (2018) Heritability: the link between development and the
10 microevolution of molar tooth form. *Historical Biology*. Taylor & Francis 30(1–2): 53–63.

11 Pregill GK, Steadman DW and Watters DR (1994) Late Quaternary vertebrate Faunas of the
12 Lesser Antilles: Historical components of Caribbean Biogeography. *Carnegie Museum of*
13 *Natural History* 30. Available at: <http://archive.org/details/bulletinofcarneg3019carn>.

14 R Core Team (2019) *R: A language and environment for statistical computing*. Vienna, Austria.
15 Available at: <https://www.R-project.org>.

16 Ray CE (1962) The oryzomyine rodents of the Antillean subregion: a thesis. PhD Thesis,
17 Harvard University.

18 Renaud S, Auffray J-C and Michaux J (2006) Conserved phenotypic variation patterns,
19 evolution along lines of least resistance, and departure due to selection in fossil rodents.
20 *Evolution*. Wiley Online Library 60(8): 1701–1717.

21 Renaud S, Michaux J, Jaeger J-J and Auffray J-C (1996) Fourier analysis applied to
22 *Stephanomys* (Rodentia, Muridae) molars: nonprogressive evolutionary pattern in a gradual
23 lineage. *Paleobiology* 22(02): 255–265.

- 1 Ricklefs RE and Bermingham E (2007) The Causes of Evolutionary Radiations in
2 Archipelagoes: Passerine Birds in the Lesser Antilles. *The American Naturalist* 169(3): 285–
3 297: doi:10.1086/510730.
- 4 Rohlf FJ (2004) tpsDig-thin plate spline digitizer, version 1.40. *State University of New York*
5 *at Stony Brook, New York.*
- 6 Rohlf FJ and Slice D (1990) Extensions of the Procrustes method for the optimal
7 superimposition of landmarks. *Systematic Biology* 39(1): 40–59.
- 8 Roughgarden J (1995) *Anolis lizards of the Caribbean: ecology, evolution, and plate tectonics.*
9 Oxford University Press.
- 10 Rouse I and Faber Morse B (1999) *Excavations at the Indian Creek Site, Antigua, West Indies.*
- 11 Russell EL, Chiang LH and Braatz RD (2000) Canonical Variate Analysis. *Data-driven*
12 *Methods for Fault Detection and Diagnosis in Chemical Processes.* Springer, 81–95.
- 13 Saitou N and Nei M (1987) The neighbor-joining method: a new method for reconstructing
14 phylogenetic trees. *Molecular biology and evolution* 4(4): 406–425.
- 15 Schlager S (2013) Morpho: Calculations and visualisations related to Geometric
16 Morphometrics. *R package version 0.23* 3: 195–220.
- 17 Scrucca L (2016) Genetic algorithms for subset selection in model-based clustering.
18 *Unsupervised Learning Algorithms.* Springer, 55–70.
- 19 Siegel PE (1989) *Early ceramic population lifeways and adaptive strategies in the Caribbean.*
20 British Archaeological Association.
- 21 Siegel PE, Jones JG, Pearsall DM, Dunning NP, Farrell P, Duncan NA, et al. (2015)
22 Paleoenvironmental evidence for first human colonization of the eastern Caribbean.
23 *Quaternary Science Reviews* 129: 275–295.

1 Steadman DW, Pregill GK and Olson SL (1984) Fossil vertebrates from Antigua, Lesser
2 Antilles: Evidence for late Holocene human-caused extinctions in the West Indies. *Proceedings*
3 *of the National Academy of Sciences* 81(14): 4448–4451: doi:10.1073/pnas.81.14.4448.

4 Stoetzel E, Cornette R, Lalis A, Nicolas V, Cucchi T and Denys C (2017) Systematics and
5 evolution of the *Meriones shawii/grandis* complex (Rodentia, Gerbillinae) during the Late
6 Quaternary in northwestern Africa: Exploring the role of environmental and anthropogenic
7 changes. *Quaternary Science Reviews*. Elsevier 164: 199–216.

8 Stouvenot C and Randrianasolo A (2013) *Matières premières lithiques des sites mésoindien et*
9 *néoindien de la Baie Orientale à Saint-Martin (Petites Antilles)*. Editions de la maison des
10 sciences de l’Homme.

11 Trouessart E-L (1885) *Note sur le rat musqué (“Mus pilorides”) des Antilles, type du sous-*
12 *genre “Megalomys”(Trt) et la place de ce sous-genre dans le groupe des rats américains ou*
13 *Hesperomyeae*". G. Masson.

14 Turvey ST, Weksler M, Morris EL and Nokkert M (2010) Taxonomy, phylogeny, and diversity
15 of the extinct Lesser Antillean rice rats (Sigmodontinae: Oryzomyini), with description of a
16 new genus and species. *Zoological Journal of the Linnean Society* 160(4): 748–772.

17 Valenzuela-Lamas S, Baylac M, Cucchi T and Vigne J-D (2011) House mouse dispersal in Iron
18 Age Spain: a geometric morphometrics appraisal. *Biological Journal of the Linnean Society*
19 102(3): 483–497.

20 van Dam J (1996) Stephanodonty in fossil murids. *Advances in morphometrics*. Springer, 449–
21 461.

22 Vázquez-Domínguez E, Garrido-Garduño T and Calixto-Pérez E (2020) Climate Change
23 Impact at the Genetic Level: Patterns in the Couesi’s Rice Rat (*Oryzomys couesi*).
24 *Conservation Genetics in Mammals*. Springer, 301–329.

- 1 Vickery KD, Theler JL and Shane III OC (2016) Archaeological Remains of the Rice Rat
2 (Oryzomys) as a Climatic Proxy in the American Midwest. *The Wisconsin Archaeological*
3 *Society* 97(2): 49–80.
- 4 Vigne J-D and Valladas H (1996) Small mammal fossil assemblages as indicators of
5 environmental change in northern Corsica during the last 2500 years. *Journal of archaeological*
6 *science* 23(2): 199–215.
- 7 Whittaker RJ and Fernández-Palacios JM (2007) *Island biogeography: ecology, evolution, and*
8 *conservation*. Oxford University Press.
- 9 Wilkinson MJ, Marshall LG, Lundberg JG and Kreslavsky MH (2010) Megafauna environments
10 in northern South America and their impact on Amazon Neogene aquatic ecosystems.
11 *Amazonia, Landscape and Species Evolution: A Look into the Past*. Wiley-Blackwell, Oxford
12 162–184.
- 13 Wing ES (2001a) The sustainability of resources used by native Americans on four Caribbean
14 islands. *International Journal of Osteoarchaeology* 11(1-2): 112–126.
- 15 Wing ES (2001b) Native American use of animals in the Caribbean. *Biogeography of the West*
16 *Indies: Patterns and Perspectives, Second Edition*. CRC Press, 481–518.
- 17 Wing ES and Wing SR (1995) Prehistoric ceramic age adaptation to varying diversity of animal
18 resources along the West Indian archipelago. *Journal of Ethnobiology* 15: 119–148.

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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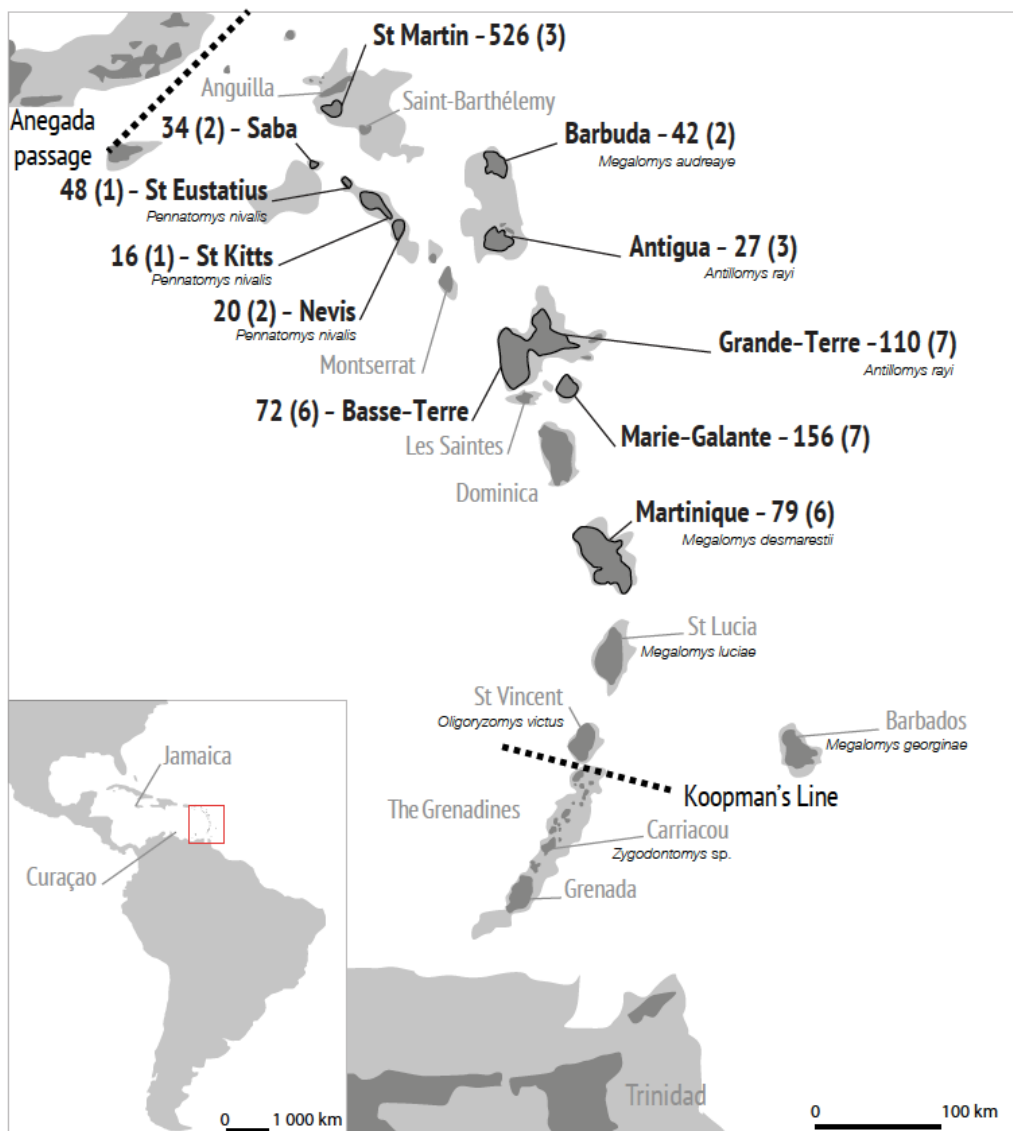
1 **Table legend:**

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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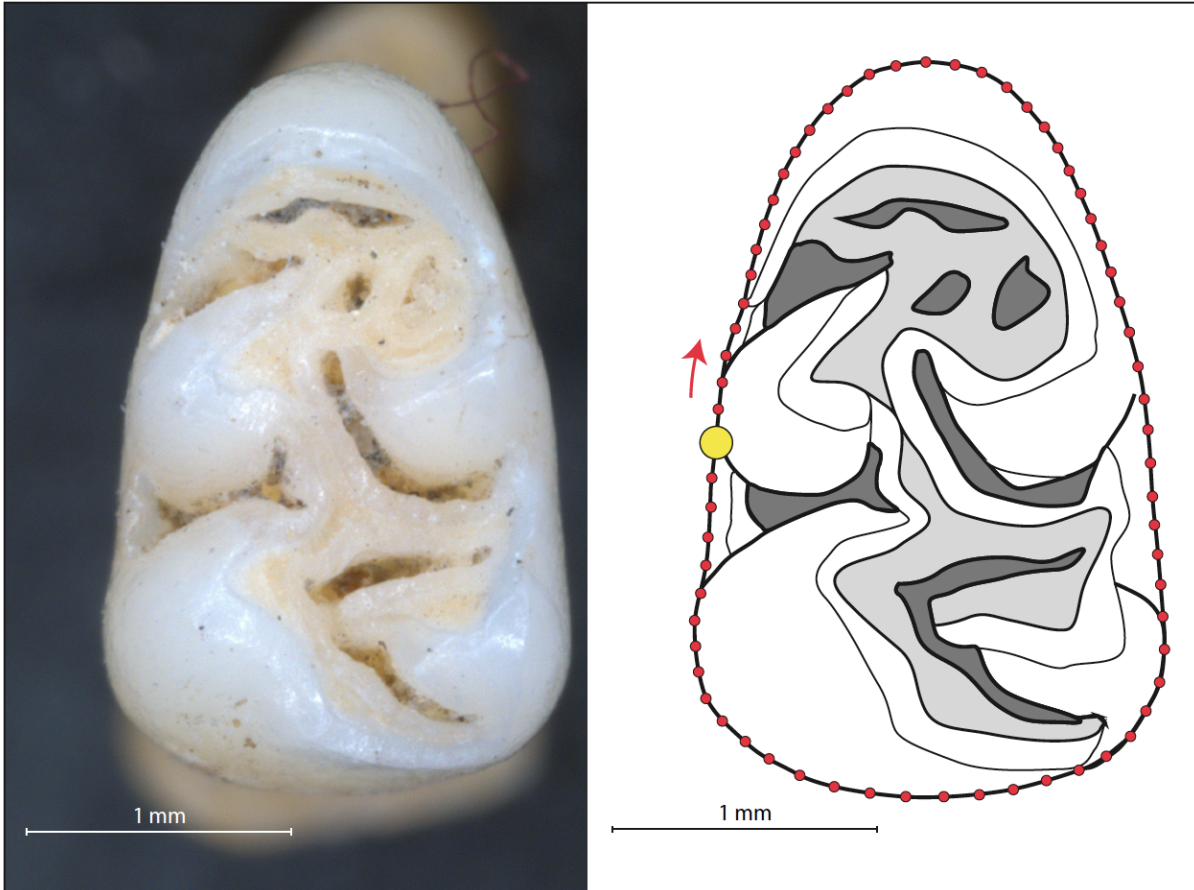
5 **Figures legends:**

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 Aneгада passage (Jany et al., 1990) and in the South Koopman's Line (Genoways et
11 al., 2010).



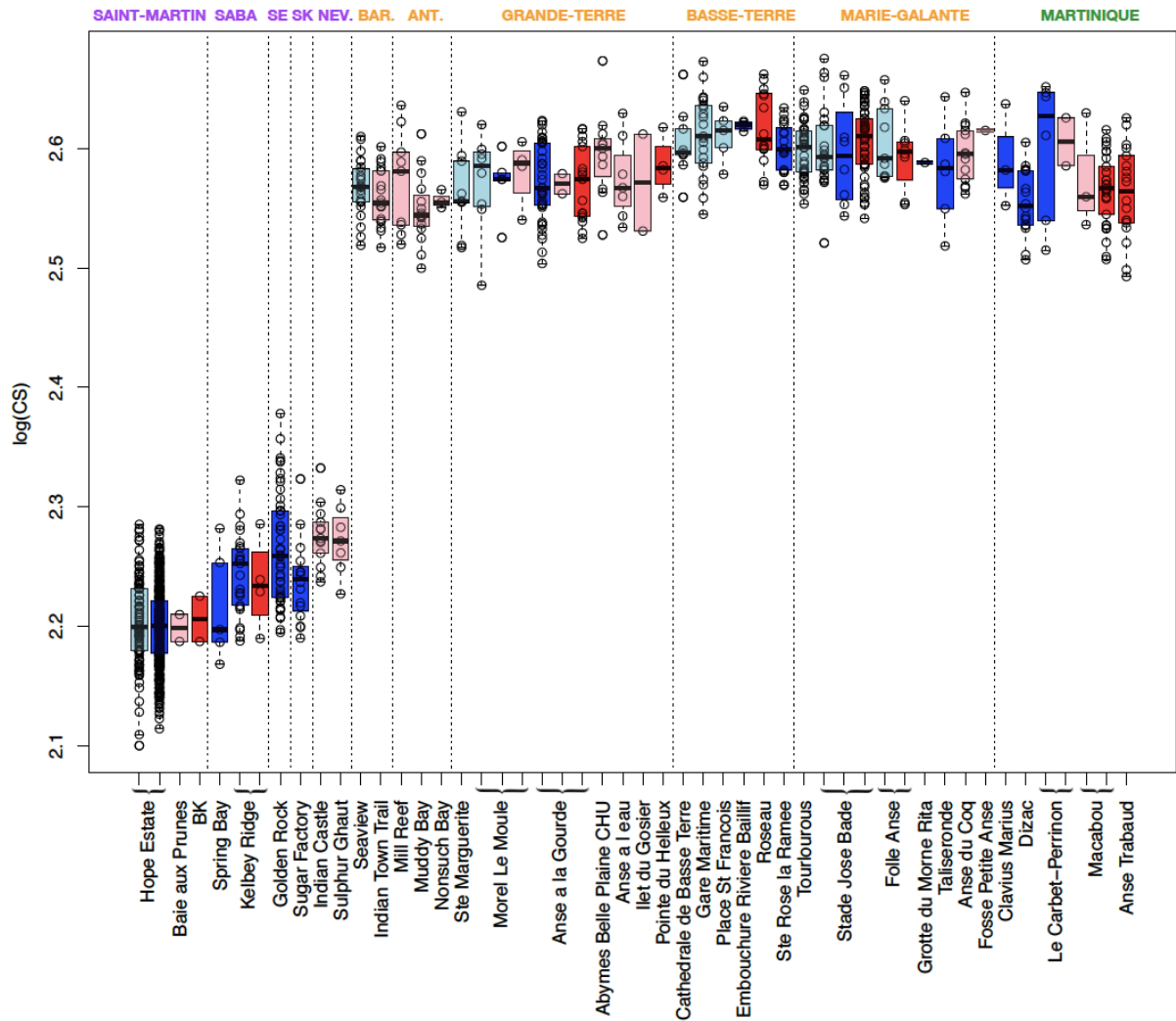
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1 **Figure 2** - Left: Occlusal view of a first lower molar of a Lesser Antillean rice rat (specimen SRA-Guadeloupe-
2 HE-089-D from Hope Estate, Saint-Martin). Right: Geometric morphometric protocol including one landmark
3 (large yellow dot) and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



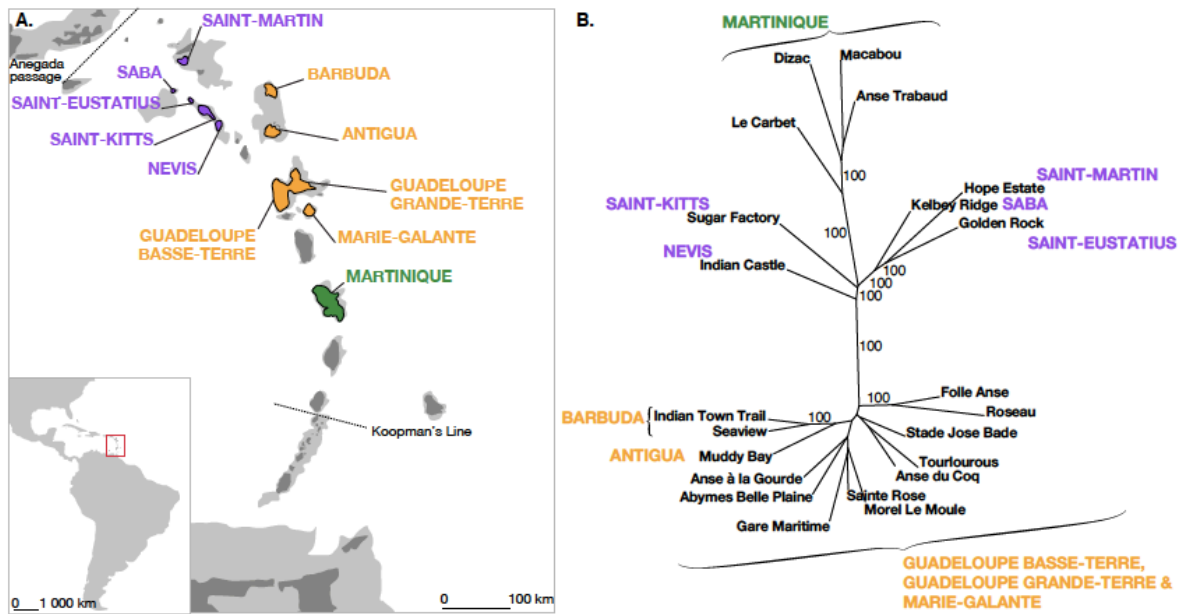
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1 **Figure 3** - Size variation between rice rat populations of the Lesser Antilles. Boxplots of the log-transformed
 2 centroid size of the lower M1. Specimens were grouped by island, site and chronological occupation phase. In
 3 light blue: Early 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).

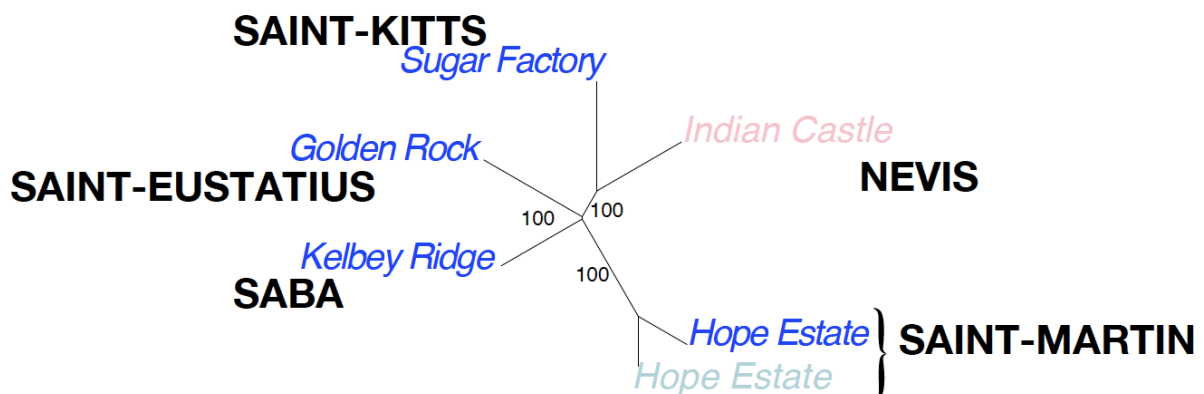


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1 **Figure 4 - A. Phenotypic relationship between sites across the Lesser Antilles.** Mean branch lengths neighbor-
 2 joining network of the bootstrapped Mahalanobis distances (1000 replicates) with mention of the bootstrap
 3 percentages above 50%. 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.

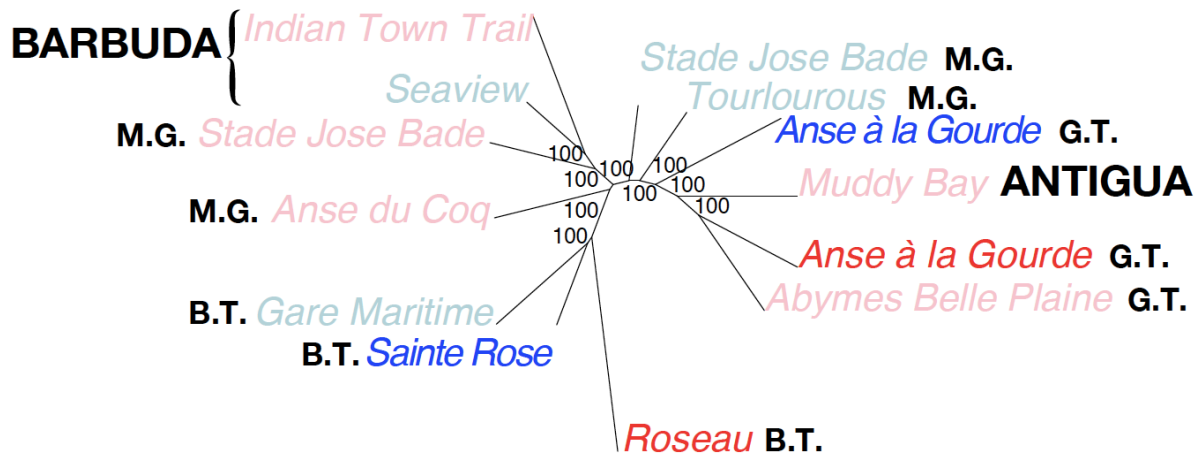


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 7 **Figure 5 - Phenotypic relationship between sites of the Northern islands.** Mean branch lengths neighbor-
 8 joining network of the bootstrapped Mahalanobis distances (1000 replicates) with mention of the bootstrap
 9 percentages above 50%. Site 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.



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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.



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