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## INITIAL OBSERVATIONS OF THE SUBFOSSIL OF PARTIALLY EXTINCT FAUNA FROM TINTAMARRE ISLAND (ANGUILLA BANK, LESSER ANTILLES)

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#### ABSTRACT

Although there is an increasing amount of subfossil data available that documents the effects of past human impact on the biodiversity of the West Indies, many islands remain poorly documented, if at all. The palaeontological study of an assemblage of terrestrial mollusk shells and bone remains recovered on the surface level of two cave deposits, *Trou de Souris* 1 and 4, provides the first data on the past biodiversity of Tintamarre Island (northern Lesser Antilles). The results indicate the presence of at least six vertebrate taxa and a possible six terrestrial snail species that are no longer present on the island. As it was not possible to excavate the deposits from which these assemblages were collected we currently lack a chronological framework to interpret the collected data. However, based on phenomena observed from several other islands in the Lesser Antilles, we propose several hypotheses linking the local extinction of these species to human activity on Tintamarre throughout the last few centuries.

Keywords: Antilles; extinction; island; palaeoontology; zooarchaeology.

### RÉSUMÉ

# PREMIÈRES OBSERVATIONS CONCERNANT LA FAUNE SUBFOSSILES ET PARTIELLEMENT ÉTEINTE DE L'ÎLE DE TINTAMARRE (BANC D'ANGUILLA, PETITES-ANTILLES)

Un nombre important d'études de restes vertébrés archéologiques et paléontologiques des Petites Antilles documentent l'effet de l'impact humain ancien sur l'érosion de la biodiversité. Pour autant, le registre fossile de nombreuses iles reste peu ou pas documenté. La présente contribution apporte les premières données concernant la biodiversité animale terrestre passée de l'îlet Tintamarre, dans le nord des Petites Antilles, sur la base de l'étude paléontologique d'un ensemble de coquilles de mollusque terrestre et d'ossements recueillis en surface de deux grottes : les Trou de Souris 1 et 4. Les résultats obtenus mettent en évidence la présence passée et donc la disparition de l'îlet de 6 espèces de vertébrés ; ils suggèrent également la disparition d'un nombre égal de taxons de mollusques terrestres. Des fouilles n'ayant pas été menées, aucun cadre chronologique n'a pu être établi pour situer ces disparitions dans le temps. Toutefois, sur la base des connaissances établies sur les autres îles des Petites Antilles, plusieurs hypothèses mettant ces disparitions en relation avec les activités humaines menées sur l'îlet au cours des derniers siècles sont proposées.

Mots-clés : Antilles; archéozoologie; extinction; île; paléontologie.

#### 1 1 - Introduction

The increasing volume of subfossil material recovered from across the globe provides 2 substantial evidence that human activities have acted as the major driver of faunal 3 biodiversity erosion across the Holocene (Ceballos et al., 2015; Ceballos et al., 2017). It is 4 now clear that human activity has led to dramatic changes in the environment and ultimately 5 6 to species extinction, and that this impact has been greater and faster than that of natural 7 events. Among all geographic areas, islands are those that are the most impacted by humans, and island fauna often suffers from intense alteration following the initial colonization and 8 subsequent anthropization of their primary environment (Olson & James, 1982; 9 Steadman, 1995; Alcover et al., 1998). The Lesser Antillean islands are a good model of the 10 impact of past human colonization on insular environments, including important evidence of a 11 massive extinction event of vertebrate species following the rapid implementation of modern 12 agricultural practices during the colonial period (Steadman et al., 1984; Bochaton, 2016; 13 14 Boudadi-Maligne et al., 2016). These islands also demonstrate the predominance of humaninduced extinction over those related to the natural changes in climate since the end of the 15 Pleistocene (Bailon et al., 2015; Stoetzel et al., 2016). However, despite the continual 16 increase in the knowledge of the Holocene biodiversity of Caribbean islands, information 17 remains localized, concentrated on some islands while other remain poorly investigated. The 18 result is that it is presently difficult to have an accurate understanding of the general processes 19 20 impacting this region because only a few direct comparisons between islands can be drawn. For instance, in the Lesser Antillean insular chain that includes the southern part of the West 21 22 Indies, Guadeloupe (Bochaton et al., 2015; Boudadi-Maligne et al., 2016; Stoetzel et al., 2016; Bochaton et al., 2016), Barbuda (Etheridge, 1964; Watters et al., 1984; Pregill et 23 al., 1994), Antigua (Steadman et al., 1984; Pregill et al., 1988) and Anguilla (Cope, 1883; 24 25 Pregill et al., 1994; Roughgarden, 1995; Kemp & Hadly, 2016), the islands have been the

object of many palaeontological studies, whereas the past biodiversity of most other islands 26 still remain unknown. The Anguilla bank (fig. 1-A) is an unusual case, as one of its main 27 islands (Anguilla) has been heavily studied, whereas the past biodiversity of the Saint Martin 28 (St. Martin) and Saint Bartholomew (St. Barth) islands remain poorly understood. In St. 29 Martin this is due to the intense destruction of its palaeontological and archaeological cave 30 deposits over the two last centuries. The caves of St Martin and their sedimentary infillings 31 have been mostly destroyed, first from phosphate exploitation, and later from real estate 32 development (Auffenberg, 1958; Hummelinck, 1981; McFarlane & MacPhee, 1993). The 33 fact that most limestone caves are near the coast make them especially susceptible to 34 35 destruction from development related to coastal mass tourism installations and private residences (Genoways et al., 2007). The effect is that very little palaeontological data has 36 been collected on St. Martin Island and only two sites are known to contain bones preserved 37 38 in their sedimentary infilling: the caves of Devil's Hole and of Cuckoo Hole near Pelikankey (Cope, 1883; Auffenberg, 1958). However, the recovered palaeontological material was 39 mostly composed of remains of the now-extinct giant hutia, Amblyrhiza inundata Cope, 1868 40 with nearly no remains of other vertebrate taxa present (Cope, 1883). Nevertheless, some 41 open-air archaeological sites do exist on St. Martin (Bonnissent, 2008) containing vast 42 quantities of fossil remains: Hope Estate (Grouard, 2004; Newsom & Wing, 2004), Anse des 43 Pères (Hofman & Hoogland, 1999; Nokkert, 1999), Norman Estate (Hofman & 44 Hoogland, 1999; Nokkert, 1999), and Baie aux Prunes (Grouard, 2005; Bonnissent, 2008). 45 Still, despite having been the object of some zooarchaeological study, these sites were never 46 exhaustively studied from a palaeontological point of view and provide limited information 47 on the past biodiversity of the island. These substantial limitations in our knowledge of the 48 biodiversity of St. Martin also apply to its nearest island neighbor; the Island of Tintamarre 49 less than 3km away from the northeast coast of St. Martin (fig. 1-B). 50

Tintamarre is a small island of 0.8 km<sup>2</sup> entirely composed of limestone (Dugain et al., 1989). 51 52 This island is part of the Anguilla bank, mainly composed of the islands of St. Martin, Saint-Barthelemy, and Anguilla that are currently separated by areas of sea less than 30m deep, and 53 during the Late Pleistocene formed a single island (Christman, 1953). Tintamarre is nearly 54 flat with a maximum elevation of 30m and is particularly dry due to a combination of low 55 precipitation and a porous limestone substrate. The vegetation of Tintamarre includes the 56 remnant of a dry deciduous forest with numerous xerophytes and succulent plant species, part 57 of a semi-deciduous forest on the plateau with lignum vitae (Gaiacum officinale) and water 58 mampoo (Pisonia subcordata), and finally salt-tolerant trees like manchineel (Hippomane 59 60 mancinella) and seagrape (Coccoloba uvifera) near the lagoons and beaches (Impact Mer, 2020). Nothing is currently known about the past biodiversity of Tintamarre but its 61 modern faunal diversity is extremely poor. Tintamarre is currently occupied only by around 62 63 33 vertebrate species, and with no more than seven species of terrestrial mollusks discovered by the collecting missions carried out in the second part of the twentieth century (Hovestadt & 64 65 Neckheim, 2020). Initially only four taxa in the families Gastocoptidae and Pupillidae were known from the material collected in 1949 by A. Hummelinck (Hummelinck, 1981) and 66 published by Haas (1960), before three new taxa were added after the recent review of the 67 collections made in the 1970s by Hummelinck (Hovestadt & Neckheim, 2020). Mammals are 68 currently represented by at least three species: goats (*Capra hircus*), black rats (*Rattus rattus*), 69 and house mice (Mus musculus) (Brown, 2008, pers. obs.). Brown rats (Rattus norvegicus) 70 may have once been present but recent trapping campaigns have demonstrated they are not 71 72 currently found on Tintamarre (Lorvelec et al., 2013; Lorvelec et al., 2017). Mongooses and cats are absent from the Island. In respect to reptiles, the Tintamarre islet is currently occupied 73 by five species of lizards: the Anguilla Bank ameiva (Pholidoscelis plei), the Anguilla Bank 74 tree anole (Anolis gingivinus), the Anguilla Bank skink (Spondylurus powelli), the 75

Sphaerodactyle of St. Martin (Sphaerodactylus parvus), and the green iguana (Iguana iguana) 76 77 (Powell & Henderson, 2012; Lorvelec et al., 2017). A single tortoise species is also present, the red-footed tortoise (Chelonoidis carbonaria) (Powell & Henderson, 2012). The island is 78 79 currently home to a total of 24 different bird species. Tintamarre hosts several species of marine birds and is classified as an Important Bird Area for breeding populations of Red-80 billed Tropicbird (Phaethon aethereus), Brown Noddy (Anous stolidus), Audubon's 81 Shearwater (Puffinus lherminieri) and a few other seabirds (Collier and Brown, 2008, 82 83 Leblond, 2012). It also hosts a small number of terrestrial bird species including doves (Zenaida aurita), passeriforms (e. g. Elaenia martinica, Tyrannus dominicensis, Coereba 84 85 flaveola, Loxigilla noctis, and Grassquit (Melanospiza bicolor) (Leblond, 2003; eBird, 2020). 86 No amphibians are currently present on the island.

The low levels of biodiversity on Tintamarre are contrasted by those of the nearby St. Martin 87 Island (Genoways et al., 2007; Yokoyama, 2013; De Massary et al., 2017). This difference 88 may be due to the species-area relationship (e.g. Ricklefs and Lovette, 1999), but may also be 89 a result of human impact, including intensive environmental modification. The latter 90 hypothesis matches the historical data of the past use of Tintamarre Island, which despite 91 being currently uninhabited has been subject to occupation and exploitation. The first 92 evidence of occupation dates back to the beginning of the 18th century for the production of 93 lime, as well as a high likelihood of forest exploitation for fuel (Lafleur, 1990). Between 1902 94 and 1931 following the installment of Diederik Christian as the "King of Tintamarre", the 95 small island hosted around 150 people and was subject to an intense level of agricultural 96 97 activity in comparison to its size (Hartog, 1981). At that time the island was home to about 60-70 cattle and 540 sheep, in addition to cotton being cultivated (Hartog, 1981). In 1931 the 98 island was sold to Louis Fleming, whose family still owns the inner part of the island. The 99 100 island was first rented to be used as an airport by the "Compagnie Aérienne Antillaise" until

1947 (Casius, 2005). At that time the island was only occupied by some employees of the 101 102 company, and is since free of all permanent human occupation although tourists still frequent the beach. There is also some sparse evidence of an occupation of the island during the pre-103 104 Columbian era, but this needs to be described with greater precision (Hénocq, 2019). The impact of each different phases of occupation has remained until now completely unknown, 105 106 as there was no data available on any subfossil material from Tintamarre. The present study 107 begins to start filling this gap in knowledge by providing the first data on the past biodiversity of Tintamarre Island based on the study of subfossil remains collected from two fossil-bearing 108 cave deposits on the island. 109

#### 110 2 - MATERIALS AND METHODS

In order to survey the caves of St Martin, members of our team visited Tintamarre Island in 111 112 March 2016 and described several caves that included two sites identified as being of palaeontological interest: the caves of Trou de Souris 1 and Trou de Souris 4 (Lenoble et 113 al., 2017). During this first visit samples of bone remains were collected from the floor of 114 each of these two cavities. The preliminary study of these samples revealed they were likely 115 to be quite ancient as well as containing several species that are no longer present on 116 Tintamarre. It was therefore of interest to conduct excavations in order to investigate the 117 composition of the past biodiversity of Tintamarre within a stratigraphic and chronological 118 framework. However, because of administration related to the ownership of the island it has 119 been impossible to obtain an excavation permit. We visited the island again in 2019 to collect 120 121 further surface samples at the two sites and decided to publish the study of these assemblages pending future excavations. The material we describe here is thus probably a minor fraction 122 123 of the full palaeontological content of these sites but it still provides some interesting preliminary data on the past biodiversity of Tintamarre. 124

The site of the *Trou de Souris 1* (18°07'22.26''N, 62°58' 31.368''O) (TS1) is the first of a 125 group of five caves located on Tintamarre in the east part of the Island, near the Mice Hole 126 locality (fig. 1-C). This small cave is the lateral chamber of a banana hole that lies between 127 one and two meters below the topographic surface; the chamber is a dozen meters long, and 128 two to three meters wide (fig. 1-D). Its floor is composed of loose clay sediment covered by 129 many vertebrate bones. The bedrock of the cavity is not visible which suggests the existence 130 131 of a sedimentary infilling of unknown depth. The site of the Trou de Souris 4 Cave (18°07'22.728"'N, 62°58' 31.62"'O) (TS4) is located nearby TS1 (fig. 1-C). The cave is at a 132 depth of six to seven meters and is accessible through a narrow shaft. It is six to seven meters 133 134 long and four meters wide (fig. 1-E). The cave floor is similar to that of Trou de Souris 1, including the scattered small vertebrate bones on the surface. These two caves are currently 135 unoccupied by bats as evidenced by the absence of decaying organic remains on the floor, and 136 overall seem to present all the suitable characteristics for the preservation of subfossil 137 assemblages. At both sites the bone and shell samples were collected by hand from the floor 138 and no sieving was conducted. The collected remains were not sampled for isotopic 139 [radiometric] dating as their probable historic/colonial origins (see Discussion) would render 140 14C dating impossible. Additional snail shells were hand-collected from the crevices in the 141 limestone pavement on the rock surface near Trou de Souris 1 (SXM-009: 18°07'22.26''N, 142 62°58' 31.368''O) and in several other outdoor localities: near the northeastern point of the 143 island (SXM-012: 18°07'22.296''N, 62°58'27.047''O), above the northern cliffs (where a soil 144 sample was also taken and sorted under the microscope) (SXM-013 : 18°07'25.536''N, 145 62°58' 37.92''O; SXM-014 : 18°07'22.44''N, 62°58' 47.459''O), close to the old sheepfold 146 (SXM-015: 18°07'04.476''N, 62°59'03.227''O), and from Baie Blanche beach (SXM-016: 147 18°07'0.48''N, 62°59' 14.892''O). 148

Bone and terrestrial snail shell remains recovered in Tintamarre and from the *Trou de Souris* caves were identified using the West Indian landsnail shell and osteological collections of the PACEA laboratory (Bordeaux University, France), the comparative anatomy collection of the *Muséum national d'Histoire naturelle* (Paris, France) and appropriate published identification criteria cited throughout the text. Vertebrate bone remains were quantified; terrestrial snail shells were recorded as only presence/absence for each locality.

155 **3 - RESULTS** 

During the two surveys of Tintamarre and the sites of *Trou de Souris* 1 and 4, 519 vertebrate bone remains and many fragmented or complete shells of terrestrial snails were recovered (Tabs. 1 & 2).

#### 159 3.1 - VERTEBRATE BONE REMAINS (TAB. 1)

Most of the mammal bones collected at both sites were attributed to unidentified rodents 160 (N=76) but we still were able to identify some cranial, mandibular, and dental remains with 161 more precision. Among these remains is a nearly complete right mandible (fig. 2-B) identified 162 as Rattus rattus (Linnaeus, 1758). Some rodent post-cranial remains were also identified as 163 Mus musculus (Linnaeus, 1758) on the basis of their very small size. This is further confirmed 164 by the presence of a mandible bearing two embedded molars (m1 and m2). In addition to 165 166 these two fairly common rodents, four dental remains were attributed to an endemic Lesser 167 Antillean rodent, Pennatomys nivalis Turvey, Weksler, Morris, and Nokkert, 2010 (fig. 2-C, D, E), from the criteria described by Turvey et al. (2010). The two M1 (complete with little 168 wear) may be identified by: the presence of three alveolar roots, the absence of or a much 169 170 reduced accessory root, an undivided anterocone (anteromedian flexus absent see fig. 2-D), a well-developed mesoloph (see fig. 2-C), and a very small posteroflexus (notch at posterior 171 margin of metacone see fig. 2-D). In addition, the position of the posterior border of the 172

zygomatic arch is slightly anterior to the most anterior alveolus of the M1. The M2 was 173 174 broken but its three roots were visible and the mesoflexus comprised a single internal fossette (see fig. 2-E). The final rodent remain of interest was a mandible bearing a much worn M1 175 with two large roots and two accessory roots. The material was too poorly preserved to take 176 precise measurements of the dental rows, however, the complete mandibular and maxillary 177 rows probably would not have exceeded 7mm in length. This would be close in size to 178 179 Pennatomys nivalis (respectively 6.61 and 6.12mm; Turvey et al., 2010) and quite unlike the other forms of native rodents present in the north of the Lesser Antilles, namely Antillomys 180 *rayi* (> 9mm; Brace et al., 2015; Goedert et al., 2020). 181

Among the other mammal taxa, 28 remains were identified as *Oryctolagus cuniculus* (Linnaeus, 1758) including a complete mandible (fig. 2-A). Some remains of Caprinae (phalanx and petrosal bones) were also identified but no diagnostic elements were present that would have allowed a specific identification as either *Capra* or *Ovis*. An unidentified Phyllostomid bat was represented by a single clavicle, and a cat canine (*Felis catus*; (Linnaeus, 1758)) and a probable lower incisor of Agouti (*Dasyprocta leporina*; Linnaeus, 1758) was also present.

189 Squamates were represented by four taxa; at least one snake and three lizards. The snake remains comprise an assemblage of 109 colubrid snake vertebrae (fig. 2-F) plus a few cranial 190 remains. The morphology of the identified trunk vertebrae are similar to those of Alsophis 191 rijgersmaei Cope, 1869 (see Bochaton et al., 2019a) but the diverse morphological variability 192 193 observed in the assemblage precludes a definitive identification and limits attribution to the level of the genus Alsophis. Vertebrae with morphological criteria of the genus 194 195 Erythrolamprus (see Bochaton et al., 2019a) are however absent from the assemblage. It is possible that the morphological variability of the fossil vertebrae of Tintamarre may 196 correspond to several species, as has been proposed for assemblages in Guadeloupe 197

(Bochaton et al., 2019, a) but further study of the Antillean colubrid snakes vertebral 198 199 morphology should be carried out to better understand the intraspecific and ontogenetic variability. Lizard remains are mostly identified as anoles (N=90), the remains primarily 200 201 comprising dentaries of a size similar to the St Martin anole currently present on Tintamarre, Anolis gingivinus Cope, 1864. These bones bear a series of pleurodont teeth slightly labialo-202 lingually flattened with tricuspid posterior teeth and monocuspid anterior teeth. Ground 203 204 lizards of the genus Pholidoscelis Fitzinger, 1843 are represented by 17 cranial remains including several dentaries (fig. 2-H). The Meckel groove is fully open on these bones, and 205 the dental region is slightly arched and bears a heterodont dentition with teeth increasing 206 207 posteriorly in size (Bochaton et al., 2019, b). A sample of 62 gecko bones were identified to the genus Thecadactylus Goldfuss, 1820. The dentaries of this gecko (fig. 2-G) are recognized 208 209 by their homodont dentition composed of a high number (30-50) of monocuspid, slender, 210 slightly blunt teeth; a ratio inferior to 4 between the dental length (in mm) and the number of teeth; and the extension of the lateral coronoid facet that reaches the level of the last dental 211 212 position (Bochaton et al., 2018). The gecko represented by these remains is now absent from Tintamarre. Four fragments of tortoise shell (costal and neural plates) have been identified but 213 do not bear any distinctive criteria. We propose a tentative attribution to Chelonoidis 214 215 *carbonaria* (Spix, 1824) as this tortoise is still present on the island. A single remain (a tibiofibula) of a small amphibian whose size and overall morphology is similar to members of the 216 genus Eleutherodactylus Duméril and Bibron, 1841 was also identified. 217

Nine bird remains representing two species of Columbidae (*Columbina passerina* (Linnaeus, 1758), *Zenaida* cf. *aurita* (Temminck, 1809), and the passeriform *Margarops fuscatus*(Vieillot, 1808) have been collected across the two sites (Tab. 1). These bones were identified
from their morphological similarity to modern specimens. *Zenaida* cf. *aurita* is represented by
a single fragment of ulna and was identified from the morphology of the *condylus dorsalis*

*ulnae* (*sensu* Baumel and Witmer, 1993) which matches that of modern *Zenaida aurita*. The
latter species is the only *Zenaida* species to have been observed within the last few years on
Tintamarre (eBird, 2020).

226 3.2 - TERRESTRIAL SNAIL SHELLS (TAB. 2)

Twelve morphotypes corresponding to at least eleven species of terrestrial snail have been identified from all samples collected in both the caves and outdoor localities. Among these eleven species, seven were found in the *Trou de Souris* caves, and three were found exclusively in the cave contexts (Tab. 2).

Annulariidae shells were collected at the majority of collection points but were only 231 232 represented by old or fossil (fully mineralized) specimens. Two species are represented; most specimens are of a medium to small-size, ranging from an elongate conic shape (fig. 3-A) to a 233 short conic shape (fig. 3-B), both displaying equally developed spiral rounded cords and axial 234 erected lamellae fusing to form tufts in the sutures of the whorls. These features agree with 235 identification as Diplopoma crenulatum (Potiez & Michaud, 1835) (see also criteria in 236 Watters, 2014), the elongate morph being similar to the specimen from St. Martin illustrated 237 by Watters (op. cit. fig. 100). The short conic morph is characterized by a smaller length, 238 lower number of whorls (up to 4 <sup>1</sup>/<sub>2</sub>), more prominent spiral cords, and very developed sutural 239 tufts that are frequently broken off. All these characteristics make this morph similar to the 240 Diplopoma sulculosum species (Pfeiffer, 1852) known from the neighboring island of 241 Anguilla, although D. sulculosum has more pronounced features (see criteria in Watters, 242 243 2014). This short morph is also indistinguishable from the St. Barth specimens assigned to D. crenulatum by Questel (2017) and D. sulculosum by Hovestadt and Neckheim (2020). This 244 morph and Tintamarre's general population of D. crenulatum therefore present characteristics 245 246 that are intermediary between D. crenulatum and D. sulculosum, which raises taxonomic

questions beyond the scope of this paper. We therefore cautiously classify it here as a *D. crenulatum* subspecies. The second species of Annulariidae is represented by a few specimens collected only in *Trou de Souris* 1 and 4. These are medium-sized specimens characterized by a teardrop-shaped aperture, a dominant axial sculpture of numerous and close lamellae and minute sutural tufts formed by 1-2 expanded axial lamellae (fig. 3-C), all characters referring to the species *Chondropoma pupiforme* (Sowerby, 1843) following Watters (2014).

A perforated Sagdidae shell displaying depressed helicoids, a subcircular aperture, rounded 253 whorls, and a very fine axial striation (Shuttleworth, 1854) (fig. 3-D) is identified as 254 Hyalosagda subaquilla (Shuttleworth, 1854). This species was collected both in the caves and 255 the outdoor locations and is represented by a small number of old shells. A unique fragmented 256 257 shell of Oleacinidae is identified as Melaniella gracillima (L. Pfeiffer, 1839) (fig. 3-E), based on its slender form and flattened whorls, its sub-triangular aperture displaying a right margin 258 impressed outward, and some twenty axial cords on the last whorl (Pilsbry, 1907). The 259 260 number of intercalated striae (a dozen) permits further identification to the variety M. g. sanctithomensis (Pilsbry, 1907) that is present in the northern Lesser Antilles (Pilsbry, 1907; 261 Haas, 1962). Two old shells of a small Bulimulidae were found in Trou de Souris 4 and at one 262 outdoor locality. The occurrence of well-marked irregular axial ribs, a shiny surface and 263 almost straight sides unambiguously enable identification to the species Bulimulus lehmani 264 (Fischer, 1857) (fig. 3-F) known from Anguilla and Dog Island (Breure, 1974). Associated 265 266 with these specimens were fragments of a very large and thin Bullimulidae shell. Because of the fragmented nature of this material we were unable to identify it to a given genera or 267 268 species. Among the most frequently encountered shells are those identified as Gastropotidae. This taxon was recovered in larger quantities at the localities where the litter was sampled, 269 which facilitated the recovery of the very small shells of these snails. Three species were 270 271 identified in the recovered samples, the most abundant being Gastrocopta bardadensis

(Pfeiffer, 1852) (fig. 3-G). The shells of this species were found associated with larger shells 272 273 (Length  $\approx 2.5$  mm) with a non-bifid parietal tooth that were identified as *Gastrocopta servilis* (Gould, 1843). Smaller shells (length < 2 mm) were also found in the same contexts, with a 274 poorly developed bifid angulo-parietal tooth and lacking any infraparietal nodule, both 275 characteristics present in the species Gastrocopta pellucida (Pfeiffer, 1840) (see Characters in 276 Pilsbry, 1916-1918). Pseudopineria viequensis (Pfeiffer, 1856) is represented by both old and 277 recent shells (fig. 3-H) in the samples collected from both caves and outdoors locations. This 278 species is characterized by its relative moderate size (Length  $\approx$  5 mm), its conical oval 279 imperforate shape and the strong oblique striations that give a spiny shape to its keel 280 281 (Pilsbry, 1904). The shells collected on Tintamarre resemble the elongated variety of Pseudopineria viequensis that is common in the northern Lesser Antilles (Pilsbry, 1904). A 282 single old shell of a large pupoid, *Pupoides albilabris* (Adams, 1841) characterized by its 283 284 reflected peristome (fig. 3-I) (Pilsbry, 1948) was found in the cave of Trou de Souris 4.

#### 285 **4 - DISCUSSION**

The faunal assemblages recovered from the caves of *Trou de Souris* 1 and 4 provide evidence of the past occurrence of at least six vertebrate taxa that are no longer present on Tintamarre Island. The timing of the extinction of these taxa is difficult to establish as the studied remains were recovered on the surface and are not dated. However, the faunal composition of the subfossil assemblage, rich in non-native species introduced by Europeans, suggests at least that these assemblages mostly document relatively recent time periods, maybe the few last centuries.

The vertebrate assemblages of *Trou de Souris* 1 and 4 are mostly composed of rodent remains the majority of which (black rat and house mouse) are taxa that arrived in the Caribbean during the colonial period along with other taxa such as goats. These taxa are still present

nowadays on Tintamarre and the fossils assemblages do not provide further clues about the 296 specific date of their introduction on the island. More interesting is the case of two other 297 European mammals that are present in the Trou de Souris bone assemblage but nowadays are 298 absent on Tintamarre: the rabbit and the cat. Both of these taxa were introduced to the Lesser 299 Antilles as early as the 17<sup>th</sup> century and were likely present on Tintamarre during the first 300 third of the 20<sup>th</sup> century when the island was intensively cultivated. The occurrence of cats 301 near human settlements is the likely association of this species, and a journal article published 302 in the "Journal de Paris" the 23<sup>rd</sup> of August 1913 describing the daily life of the "King of 303 Tintamarre" mentions that he was hunting wild rabbits on the island. The disappearance of the 304 rabbit on Tintamarre could be easily explained by the absence of agricultural activities on 305 Tintamarre after the island was sold in 1931 and by the presence of rats on the Island. In 306 general rabbits tend to fail to establish feral populations in the West Indies because juveniles 307 308 are intensively predated by mongooses and rats (Du Tertre, 1654; Flux & Fullagar, 1992; Lorvelec et al., 2007). Also, from a more global point of view, rabbits are difficult to breed in 309 tropical areas (Lebas, 2005). The disappearance of cats is more difficult to explain as Muridae 310 (mice and rats) are still present on the island and would represent an important food source; 311 but there is no evidence that any population of feral cats ever existed on Tintamarre and this 312 species may have left the island at the same time as the last farmers. The final mammal of 313 probable introduced origin present in these fossil assemblages is the agouti. These rodents are 314 known to have been introduced by Amerindian populations to the Lesser Antilles (Newsom & 315 Wing, 2004; Giovas et al., 2016) and have not been previously mentioned in reports on 316 Tintamarre. The arrival date of this species on Tintamarre remains very enigmatic as well as 317 the reason for its local extinction. It might have been predated by humans and dogs but more 318 data would be needed to discuss this question further. 319

There are two wild mammals present in the assemblages of Trou de Souris 1 and 4 that are 320 now absent on Tintamarre (Pennatomys nivalis and Phyllostomidae sp.) along with one snake 321 (Alsophis sp.), one lizard (Thecadactylus sp.), and one amphibian (Eleutherodactylus sp.). 322 The occurrence of *Pennatomys nivalis* on Tintamarre is worth noting as it is the first 323 identification of this taxon outside of the St. Kitts bank (Turvey et al., 2010; Brace et 324 al., 2015). One of us (D. C.) also identified this taxon in the archaeological assemblage of 325 Hope Estate in St. Martin, which would possibly extend the distribution of this taxon to the 326 whole Anguilla bank. This taxon may also have been introduced from the nearby St. Kitts 327 bank but its native or introduced status on Tintamarre and the whole Anguilla bank cannot be 328 tested with the currently available data. Lesser Antillean rice rats (Antillomys rayi et 329 Megalomys ssp.) all became extinct after the European arrival, between the XVI<sup>th</sup> and the 330 XX<sup>th</sup> century probably following the destruction of their native environments and the 331 introduction of predators, and competitors such as the black rat (Harris, 2009 ; Goedert et 332 al., 2020). The presence of several introduced taxa and intensive agricultural activities on 333 334 Tintamarre across the last few centuries could also potentially have led to the extinction of Pennatomys nivalis on the island, an explanation also viable for the four other now-extirpated 335 taxa discovered in the Trou de Souris bone collections. There is no available record regarding 336 the modern diversity of bats on Tintamarre but we did not observe any during our exploration 337 of the caves of the island and it is possible that phyllostomid bats are no longer present. The 338 three species of birds identified in the Trou de Souris sites are relatively common birds on the 339 neighboring island of St. Martin. The Pearly-eyed Thrasher (Margarops fuscatus) and the 340 341 Common Ground Dove (Columbina passerina) have not been observed on the islet for the last decade. They are however listed as present on the island by older studies (Collier & 342 Brown, 2008). These birds could be either occasional occupants of the Island, or have 343 disappeared relatively recently. In respect to reptiles and amphibians, the extirpation of 344

Alsophis on Tintamarre is not surprising as these snakes are known to be very vulnerable to 345 346 human impact and have suffered many local extinctions in the Lesser Antilles including on the nearby island of St. Martin where the native species of these snakes is supposed to have 347 become extinct very recently (Breuil, 2002; Powell & Henderson, 2012). The extirpation of 348 Thecadactylus is more unusual as this taxon generally resists human disturbance quite well, 349 350 and there is no clear explanation for its disappearance on Tintamarre. This gecko genus is represented by an endemic species on the Anguilla bank, Thecadactylus oskrobapreinorum 351 Köhler & Vesely, 2011 and so is likely to have been present for a long time in the bank and 352 also on Tintamarre. There is no evidence for a similarly endemic species frog of the genus 353 354 Eleutherodactylus on the Anguilla banc. Such a species may have become extinct and replaced by two other lesser Antillean species: E. martinicensis (Tschudi, 1838) and E. 355 *johnstonei* Barbour, 1914. As it is not possible to identify the two frog remains found in the 356 357 Trou de Souris caves we cannot state if they belong to an introduced species or a native one. The extinction of this unidentified amphibian is however surprising and could be potentially 358 359 explained by aridification following the removal of the primary forest for agricultural purpose, or by the final abandonment of the agricultural activity of the island. 360

The other non-mammal taxa represented by bone remains collected in the fossil deposits are 361 still present on the island today. Two of them are lizard genera present on most islands in the 362 Anguilla bank (Anolis sp. and Pholidoscelis sp.) where they are typically represented by 363 endemic species (Powell & Henderson, 2012). The remaining taxon is the red-footed tortoise, 364 a non-native species that is today present on all major islands of the Anguilla bank and whose 365 366 introduction date in the West Indies is subject to much debate. Tortoises of the genus Chelonoidis were present on the Anguilla bank since the Pleistocene (Lazell, 1993) but the 367 specific attribution of these remains to Chelonoidis carbonaria remain doubtful, and this 368 369 species is absent in the Amerindian archaeological deposits of the region. An alternative

hypothesis regarding the introduction of this turtle species to the Lesser Antilles were recently
reviewed by De Massary et al. (2018), and it appears that they were most likely introduced to
most regions during the 19<sup>th</sup> century.

From a general point of view, the data collected from the Trou de Souris bone assemblages 373 indicates that the fauna of Tintamarre was probably strongly impacted by human activities 374 375 during the last few centuries although the lack of isotopic dating of the material prevents any definitive conclusions. The biodiversity profile of this island is however unusual, as although 376 it has suffered from the same extinctions that have occurred in many if not all of Lesser 377 Antillean islands (rabbit, rice rat, and the *Alsophis* snake) other unusual extinction events 378 (Thecadactylus and Eleutherodactylus) seem to point towards particularly strong 379 environmental modifications of the island. However, conversely, the endemic Anguilla Bank 380 skink (Spondylurus powelli) is still extant on the island despite skinks being nowadays extinct 381 on most of the Lesser Antillean islands (Hedges & Conn, 2012). This could be related to the 382 383 fact that the mongoose was never introduced to Tintamarre, which seems to be confirmed by our observations, and that the stone walls constructed by farmers on the island represent a 384 very suitable and protective environment for these lizards, as suggested by Lorvelec et al. 385 (2017)386

Regarding terrestrial snails, our newly collected data enriches our knowledge of the 387 biodiversity of these organisms on Tintamarre by doubling the number of taxa listed for this 388 island. With one exception, all the species collected on Tintamarre are known from the 389 390 neighboring island of St. Martin, to which this island was attached during the periods of low sea levels during the Pleistocene. The number of species recorded on Tintamarre is still 391 392 however much lower, as no fewer than 40 species of snails have been recorded on St. Martin (Hovestadt & Neckheim, 2020). The terrestrial mollusk population of Tintamarre thus forms a 393 sub-sample of the fauna of St. Martin, including calcicole (e.g. Pupoides albilabris, 394

395 Diplopoma crenulatum), xeric (e.g., Gastocopta spp.), and coastal (e.g., Pseudopineria
396 viequensis) species.

The only Tintamarre species absent from St. Martin is *Bulimulus lehmani*, a species present 397 on the island of Anguilla, while the genus *Bulimulus* is currently represented on St Martin by 398 Bulimulus diaphanus and B. guadalupensis (Breure, 1974). Bulimulus lehnmani was formerly 399 400 observed on the island of St. Martin (Coomans, 1967; Bertrand, 2001), but these records are 401 unreliable as they are not associated with a locality and this species has not been found during the systematic surveys carried out during the last few decades (Hovestadt & 402 Neckheim, 2020). In this study, we demonstrate the past presence of B. lehmani on 403 Tintamarre but this species is only represented by few old shells. The status of this species on 404 405 the island still has to be demonstrated and it could have been unintentionally introduced from Anguilla during historical times as many Tintamarre workers were Anguillan inhabitants. 406

The biogeographic distribution of Annulariidae on the Anguilla Bank is complex. One species 407 is endemic to the northern island of Sombrero (Chondropoma julieni (L. Pfeiffer, 1866)), 408 another is known to be endemic to Anguilla and the satellite islets (Diplopoma sulculosum), a 409 third species is found in Anguilla and the limestone terrain of the southern part of St. Martin 410 411 (Chondropoma pupiforme), and a final species (Diploploma crenulatum) is known only from the northern part of St. Martin but from the more southern islands of the Lesser Antilles 412 413 below Martinique. Meanwhile, the specimens found in St. Bartholomew are identified as either D. sulculosom or D. crenulatum depending on the authors (Watters, 2014; 414 415 Questel, 2017; Hovestadt & Neckheim, 2020). In this study the species of interest are the two Annulariid land snails Diplopoma crenulatum and Chondropoma pupiforme. The recovery of 416 417 C. pupiforme shells from the Tintamarre caves and its absence in outdoor localities indicates that this species is currently very rare on the islet, if not already extinct. Furthermore, this 418 record fills the gap of the distribution of this species between Anguilla and the island south of 419

420 St. Martin. The population of *D. crenulatum* collected at Tintamarre, with intermediate 421 characteristics between the St. Martin form and the Anguilla Island species (*D. sulculosum*), 422 also suggests the presence of phenotypic and geographic intergrades between species of the 423 *Diplopoma* genus within the Anguilla Bank. The distribution of Annulariidae therefore is, or 424 would have been, much less fragmented than previous data suggests.

425 It is interesting to observe that the many invasive species currently present on St. Martin and 426 more widely in the West Indies are absent from Tintamarre. These species includes: Achatinidae, e.g., Subulina octona (Bruguière, 1789), and Allopeas gracile (Hutton, 1834); 427 Polygyridae, e.g., Polygyra cereolus (Megerle von Muhlfeld, 1816); various species of 428 Streptaxidae, including Streptartemon deplanchei (Drouët, 1859) and S. glaber (L. Pfeiffer, 429 430 1849); and some Caribbean species such as the Cuban Zachrysia provisoria (Pfeiffer, 1858) or the even more widespread Bulimulus guadalupensis (Bruguière, 1789). These absences 431 show that the initial land snail community of Tintamarre is potentially well preserved, which 432 433 could reflect restrictive environmental conditions and/or the limited frequentation of the island by human populations. The character profile of a preserved fauna is, however, 434 counterbalanced by the high proportion of species represented only by old shells in the 435 collected material, such as the abundant Diplopoma crenulatum, but also the rare shells of 436 Chondropoma pupiforme, Melaniella gracillima, Pupoides albilabris, Hyalosagda 437 subaquilla, and Bulimulus lehmani for which only a single or a very small number of 438 specimens were found. The fact that the collected remains are rare and do not present the 439 characteristic appearance of recent shells suggests that these species may no longer be extant 440 441 on Tintamarre. However, the period during which the collecting was carried out, at the end of the dry season, and only a year and a half after a major cyclone, may have impacted the 442 diversity we observed. A better assessment of the current mollusk fauna of the island, 443 444 including surveys carried out under better climatic conditions, is needed to resolve this issue.

Our data also demonstrates the value of cave deposits in documenting the malacological community of the island. All identified species were found in the *Trou de Souris* caves, with the exception of the very small Gastrocoptidae and the fragments of Oleacinidae (see Tab. 2) that were difficult to collect without the sampling and washing of sediment. Moreover, several species that were not observed in outdoors locations were collected in the caves (*Chondropoma pupiforme, Pupoides albilabris*, Bulimulidae sp.). This is probably related to the better preservation condition of the shells trapped in caves.

#### 452 **5 - CONCLUSION**

Our study of the remains collected on the surface of two fossiliferous deposits on Tintamarre Island demonstrates the past occurrence of at least six vertebrate taxa as well as potentially six terrestrial snail species that are no longer present on the island. The lack of data regarding the age of the studied material prevents the association of these extinctions with any specific events but, based on events observed on several other islands in the Lesser Antilles, we propose several hypotheses linking these extinctions to a probable anthropogenic impact across the last few centuries.

It would be very interesting to build on these initial results concerning the past biodiversity of 460 Tintamarre with an additional survey aiming to document its current terrestrial malacofaune 461 and, of course, a proper excavation of the Trou de Souris caves. Such an excavation would 462 provide an opportunity for a major improvement in our current knowledge and would enable 463 (1) the addition of a chronological framework to our observations, (2) more precise 464 identification of the taxa by obtaining more material and (3) a better characterization of the 465 evolution of the biodiversity on Tintamarre. Finally, this island has proved to be very 466 interesting, as the trajectory of biodiversity seems to deviate from the usual trends observed 467

468 and could therefore be very useful in testing several hypotheses regarding past and present469 human impact on the Lesser Antillean fauna.

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#### 480 **REFERENCES**

481 482 ALCOVER J.A., SANS A. & PALMER M., 1998 - The Extent of Extinctions of Mammals on Islands. Journal of Biogeography, 25, (5), 913-918, 10.1046/j.1365-2699.1998.00246.x. 483 484 485 AUFFENBERG W., 1958 - 1958 West Indies Field Trip. unpublished typing report, University of Florida, 486 487 Miami. 488 489 490 BAILON S., BOCHATON C. & LENOBLE A., 2015 - New data on Pleistocene and Holocene herpetofauna of Marie-Galante (Blanchard Cave, Guadeloupe Islands, French West Indies): Insular 491 faunal turnover and human impact. Quaternary Science Reviews, 128, 127-137, 492 493 10.1016/j.guascirev.2015.09.023. 494 495 496 BAUMEL J.J. & WITMER L.M., 1993 - Osteologia. In J. J. Baumel, A. S. King, J. E. Breazile, H. E. Evans et J. C. Van den Berge (eds.), Handbook of Avian Anatomy: Nomina Anatomica Avium. Publications of 497

498 499	the Nuttall Ornithological Club, 23. Nuttall Ornithological Club, Cambridge, U.S.A., 45-132.
500 501 502 503	<b>BERTRAND A., 2001</b> - <i>Notes préliminaires sur les mollusques terrestres de Guadeloupe.</i> Diren Guadeloupe, Basse-Terre, 35 p. p.
504 505 506 507 508	<b>BOCHATON C., 2016</b> - Squamates du Pléistocène supérieur et de l'Holocène de l'archipel guadeloupéen : Évolution de la biodiversité et interactions avec l'Homme. PhD thesis. Muséum national d'Histoire naturelle, Paris, France, 428 p.
509 510 511 512 513 514	<b>BOCHATON C., BAILON S., INEICH I., BREUIL M., TRESSET A. &amp; GROUARD S., 2016</b> - From a thriving past to an uncertain future: Zooarchaeological evidence of two millennia of human impact on a large emblematic lizard ( <i>Iguana delicatissima</i> ) on the Guadeloupe Islands (French West Indies). <i>Quaternary Science Reviews</i> , <b>150</b> , 172-183, 10.1016/j.quascirev.2016.08.017.
515 516 517 518 519	<b>BOCHATON C., BOISTEL R., GROUARD S., INEICH I., TRESSET A. &amp; BAILON S., 2019</b> - Fossil dipsadid snakes from the Guadeloupe Islands (French West-Indies) and their interactions with past human populations. <i>Geodiversitas</i> , <b>41</b> , (12), 501-523.
520 521 522 523 524 525	<b>BOCHATON C., BOISTEL R., GROUARD S., INEICH I., TRESSET A. &amp; BAILON S., 2019</b> - Evolution, diversity and interactions with past human populations of recently extinct <i>Pholidoscelis</i> lizards (Squamata: Teiidae) from the Guadeloupe Islands (French West-Indies). <i>Historical Biology</i> , <b>31</b> , (2), 140-156, https://doi.org/10.1080/08912963.2017.1343824.
526 527 528 529 530 531 532	<b>BOCHATON C., DAZA J.D. &amp; LENOBLE A., 2018</b> - Identifying gecko species from Lesser Antillean paleontological assemblages: Intraspecific osteological variation within and interspecific osteological differences between <i>Thecadactylus rapicauda</i> (Houttuyn, 1782) (Phyllodactylidae) and <i>Hemidactylus mabouia</i> (Moreau de Jonnès, 1818) (Gekkonidae). <i>Journal of Herpetology</i> , <b>52</b> , (3), 313-320, 10.1670/17-093.
533 534 535 536 537	<b>BOCHATON C., GROUARD S., CORNETTE R., INEICH I., TRESSET A. &amp; BAILON S., 2015</b> - Fossil and subfossil herpetofauna from Cadet 2 Cave (Marie-Galante, Guadeloupe Islands, F. W. I.): Evolution of an insular herpetofauna since the Late Pleistocene. <i>Comptes Rendus Palévol</i> , <b>14</b> , (2), 101-110.
538 539 540 541	<b>BONNISSENT D., 2008</b> - Archéologie précolombienne de l'île de Saint-Martin, Petites Antilles (3300 BP - 1600 AD). thèse de doctorat. Université Aix-Marseille, Aix-Marseille, 617 p.

542 543 544 545 546	BOUDADI-MALIGNE M., BAILON S., BOCHATON C., CASAGRANDE F., GROUARD S., SERRAND N. & LENOBLE A., 2016 - Evidence for historical human-induced extinctions of vertebrate species on La Désirade (French West Indies). <i>Quaternary Research</i> , 85, (1), 54-65.
547 548 549 550 551	<b>BRACE S., TURVEY S.T., WEKSLER M., HOOGLAND M.L.P. &amp; BARNES I., 2015</b> - Unexpected Evolutionary Diversity in a Recently Extinct Caribbean Mammal Radiation. <i>Proceedings of the Royal Society B: Biological Sciences</i> , <b>282</b> , (1807), 20142371, 10.1098/rspb.2014.2371.
552 553 554 555 556	<b>BREUIL M., 2002</b> - Histoire naturelle des amphibiens et reptiles terrestres de l'archipel guadeloupéen: Guadeloupe, Saint-Martin, Saint-Barthélémy. Patrimoines Naturels, <b>54</b> . Publications Scientifiques du Muséum National d'Histoire Naturelle, France, 339 p.
557 558 559 560	<b>BREURE A.S.H., 1974</b> - Caribbean land molluscs: Bulimulidae, I. Bulimulus. <i>Studies on the Fauna of Curaçao and other Caribbean Islands</i> , <b>94</b> , 118-145.
561 562 563 564	<b>BROWN A.C., 2008</b> - Status and Range of Introduced Mammals on St. Martin, Lesser Antilles. <i>Living World, Journal of The Trinidad and Tobago Field Naturalists' Club</i> , <b>2008</b> , 14-18.
565 566 567 568	<b>CASIUS J., 2005</b> - Compagnie Aérienne Antillaise. <i>American Aviation Historical Society Journal</i> , <b>50</b> , (1), 55-66.
569 570 571 572 573	<b>CEBALLOS G., EHRLICH P.R., BARNOSKY A.D., GARCÍA A., PRINGLE R.M. &amp; PALMER T.M., 2015</b> - Accelerated Modern Human–Induced Species Losses: Entering the Sixth Mass Extinction. <i>Science Advances</i> , <b>1</b> , (5), e1400253, 10.1126/sciadv.1400253.
574 575 576 577 578	<b>CEBALLOS G., EHRLICH P.R. &amp; DIRZO R., 2017</b> - Biological Annihilation via the Ongoing Sixth Mass Extinction Signaled by Vertebrate Population Losses and Declines. <i>Proceedings of the National</i> <i>Academy of Sciences</i> , <b>114</b> , (30), E6089-E6096, 10.1073/pnas.1704949114.
579 580 581 582 583	<b>CHRISTMAN R.A., 1953</b> - Geology of St. Bartholomew, St. Martin, and Anguilla, Lesser Antilles. <i>Geological Society of America Bulletin</i> , <b>64</b> , (1), 65-96, 10.1130/0016- 7606(1953)64[85:GOSBSM]2.0.CO;2.
584 585	COLLIER N. & BROWN A., 2008 - St Martin. In D. C. Wege et V. Anadon-Irizarry (eds.), Important Bird

586 587 588	Areas in the Caribbean: Key Sites for Conservation. BirdLife Conservation Series, <b>15</b> . Cambridge, UK, 290-294.
589 590 591 592	<b>COOMANS H.E., 1967</b> - The Non-marine Mollusca of St. Martin (Lesser Antilles). <i>Stud. Fauna Cur. &amp; Car. Isl</i> , <b>23</b> , 118–145.
593 594 595 596 597	<b>COPE E.D., 1868</b> - Exhibition of bones and teeth of a large rodent from the cave deposits of Anguilla, one of the West Indian Islands. <i>Proceedings of the Academy of Natural Sciences of Philadelphia</i> , <b>1868</b> , 313.
598 599 600 601 602 603	<b>COPE E.D., 1883</b> - On the Contents of a Bone Cave in the Island of Anguilla (West Indies). Washington, Smithsonian institution, 64 p., https://archeogrid.u- bordeaux3.fr/PCR_cavites/ressources%20bibliographiques/Axe1- archeozoologie/ouvrages/Cope_1883_contents-of-bone-cave-Anguilla.pdf.
604 605 606 607 608	<b>DE MASSARY JC., BOCHATON C., BOUR R., DEWYNTER M., INEICH I., VIDAL N. &amp; LESCURE J., 2018</b> - Liste taxinomique de l'herpétofaune dans l'outre-mer français : II. Collectivité de Saint-Barthélemy. <i>Bulletin de la Société Herpétologique de France</i> , <b>166</b> , 59-78.
609 610 611 612 613	<b>DE MASSARY JC., BOUR R., DEWYNTER M., INEICH I., VIDAL N. &amp; LESCURE J., 2017</b> - Liste taxinomique de l'herpétofaune dans l'outre-mer français : I. collectivité de Saint-Martin. <i>Bulletin de la Société Herpétologique de France</i> , <b>164</b> , 37-54.
614 615 616 617 618	<b>DU TERTRE JB. (R. P.), 1654</b> - <i>Histoire générale des isles de S. Christophe, de la Guadeloupe, de la Martinique, et autres dans l'Amérique</i> . A Paris : Chez Jacques Langlois et Emmanuel Langlois, Paris, 542 p., http://archive.org/details/cihm_34860.
619 620 621 622	<b>DUGAIN J., ANDREIEFF P., WESTERCAMP D., BOUYSSE P. &amp; GARRABÉ F., 1989</b> - Carte géologique de Saint-Martin au 1:50 000. BRGM, Orléans, France, 59 p. p.
623 624 625 626	<b>EBIRD, 2020</b> - eBird: An online database of bird distribution and abundance [web application]. eBird, Cornell Lab of Ornithology. 2020.
627 628	ETHERIDGE R., 1964 - Late Pleistocene lizards from Barbuda, British West Indies. Bulletin of the

629 630	Florida State Museum, <b>9</b> , (2), 46-75.
631 632 633 634	FLUX J.E.C. & FULLAGAR P.J., 1992 - World Distribution of the Rabbit Oryctolagus Funiculus on Islands. <i>Mammal Review</i> , 22, (3-4), 151-205, 10.1111/j.1365-2907.1992.tb00129.x.
635 636 637 638 639	GENOWAYS H.H., PEDERSEN S.C., LARSEN P.A., KWIECINSKI G.G. & HUEBSCHMAN J.J., 2007 - Bats of Saint Martin, French West Indies/Sint Maarten, Netherlands Antilles. <i>Mastozoología Neotropical</i> , 14, (2), 169-188.
640 641 642 643 644	<b>GIOVAS C.M., KAMENOV G.D., FITZPATRICK S.M. &amp; KRIGBAUM J., 2016</b> - Sr and Pb isotopic investigation of mammal introductions: Pre-Columbian zoogeographic records from the Lesser Antilles, West Indies. <i>Journal of Archaeological Science</i> , <b>69</b> , 39-53, 10.1016/j.jas.2016.03.006.
645 646 647 648 649	<b>GOEDERT J., COCHARD D., LORVELEC O., OBERLIN C., CUZANGE MC., ROYER A. &amp; LENOBLE A.,</b> <b>2020</b> - Isotopic ecology and regional extirpation chronology of the extinct Lesser Antillean rat <i>Antillomys rayi. Quarternary Science Reviews</i> , <b>245</b> , 106509.
650 651 652 653 654 655	<b>GROUARD S., 2004</b> - Variation des stratégies de subsistance des Précolombiens à Hope Estate, Saint- Martin (Petites Antilles), d'après l'analyse des restes des petits vertébrés. <i>In XXIVe rencontres</i> <i>internationales d'archéologie et d'histoire d'Antibes, Petits animaux et sociétés humaines: du</i> <i>complément alimentaire aux ressources utilitaires</i> . Éditions APDCA, Antibes, France, , 451-467.
656 657 658 659 660	<b>GROUARD S., 2005</b> - Une Population De Pêcheurs-Piégeurs-Collecteurs À Baie Aux Prunes / Plum Bay, Saint-Martin, Petites Antilles. <i>In XX Congress for Caribbean Archaeology, Proceedings of the XX</i> <i>Congress for Caribbean Archaeology</i> . Dominican Republic, , 308-316.
661 662 663 664	<b>HAAS F., 1960</b> - Caribbean Land Molluscs: Vertiginidae. <i>Studies on the Fauna of Curaçao and other Caribbean Islands</i> , <b>41</b> , (41), 1-17.
665 666 667 668	HAAS F., 1962 - Caribbean Land Molluscs: Subulinidae and Oleacinidae. <i>Studies on the Fauna of Curaçao and Other Caribbean Islands</i> , 58, 1-60.
669 670 671 672	HARRIS D.B., 2009 - Review of Negative Effects of Introduced Rodents on Small Mammals on Islands. Biological Invasions, 11, (7), 1611-1630, 10.1007/s10530-008-9393-0.

673 674 675	HARTOG J., 1981 - History of Sint Maarten and Saint Martin. Jaycees, Philipsburg, Sint Marteen.
676 677 678 679	HEDGES S.B. & CONN C.E., 2012 - A new skink fauna from Caribbean islands (Squamata, Mabuyidae, Mabuyinae). <i>Zootaxa</i> , 3288, 1-244.
680 681 682 683	<b>HÉNOCQ C., 2019</b> - Prospection diachronique post-Irma, Saint-Martin, Phase 2. Rapport final d'opération, Collectivité de Saint-Martin, Saint-Martin.
684 685 686 687 688 689	HOFMAN C.L. & HOOGLAND M.L., 1999 - Archaeological investigations on St. Martin (Lesser Antilles): The sites of Norman Estate, Anse des Pères and Hope Estate with a contribution to the 'La Hueca problem'. Archaeological Studies Leiden University, <b>4</b> . Faculty of Archaeology, Leiden University, Leiden, Netherlands, 315 p.
690 691 692 693 694	<b>HOVESTADT A. &amp; NECKHEIM C.M., 2020</b> - A critical checklist of the non-marine molluscs of St. Martin, with notes on the terrestrial malacofauna of Anguilla and Saint-Barthélemy, and the description of a new subspecies. <i>Folia Conchyliologica</i> , <b>57</b> , 1-38.
695 696 697 698	<b>HUMMELINCK P.W., 1981</b> - Land and Freshwater Localities. <i>Studies on the Fauna of Curaçao and other Caribbean Islands</i> , <b>192</b> , 1-133.
699 700 701 702 703	IMPACT MER, 2020 - Évaluation de l'impact du cyclone Irma sur la flore sensible de quatre îlets de la Réserve Naturelle Nationale de Saint-Martin – Rapport final. Réserve Naturelle Nationale de Saint- Martin, Saint-Martin, 60 p.
704 705 706 707	<b>KEMP M.E. &amp; HADLY E.A., 2016</b> - Early Holocene turnover, followed by stability, in a Caribbean lizard assemblage. <i>Quaternary Research</i> , <b>85</b> , (2), 255-261, 10.1016/j.yqres.2015.12.007.
708 709 710 711	<b>LAFLEUR G., 1990</b> - <i>Saint-Martin (XVIIIe - XIX siècles), Carrefour des Antilles</i> . Saint-Martin, FeniXX réédition numérique (Mairie de Saint-Martin), 50 p.
712 713 714 715	<b>LAZELL J.D., 1993</b> - Tortoise, cf. <i>Geochelone carbonaria</i> , from the Pleistocene of Anguilla, Nothern Lesser Antilles. <i>Journal of Herpetology</i> , <b>27</b> , (4), 485-486.

716	
717	LEBAS F., 2005 - Rabbit production in tropical zones. In 3rd International Rabbit Production
718	Symposium. International Rabbit Production Symposium, Villareal, Portugal, , 1-9.
719	
720	
721	LEBLOND G., 2003 - Les oiseaux marins nicheurs de Guadeloupe et de Saint-Martin et de Saint-
722	Barthélemy. Rapport BIOS/DIREN, BIOS/DIREN, Guadeloupe, 101 p.
723	
724	
725	LENOBLE A., QUEFFELEC A. & COCHARD D., 2017 - Potentiel archéologique et paléontologique des
726	cavités naturelles de Saint Martin. CNRS, DAC Guadeloupe, Basse-Terre, Guadeloupe, 56 p. p.
727	
728	
729	LORVELEC O., BARRÉ N., CHALIFOUR J., TEYNIÉ A., PISANU B. & HEDGES S.B., 2017 - Discovery of a
730	population of Spondylurus powelli (Squamata: Mabuyidae) on Île Tintamarre (Saint-Martin, French
731	Antilles) and comments on relationships among skinks of the Anguilla Bank. Caribbean Herpetology,
732	<b>59</b> , 1-8.
733	
734	
735	LORVELEC O., LE QUILLIEC P. & PISANU B., 2013 - Compte rendu de mission sur Saint-Martin et les
736	îlets de sa réserve naturelle nationale (1er-15 mars 2013). INRA / MNHN, Saint-Martin, 1-35 p.
737	
738	
739	LORVELEC O., PASCAL M., DELLOUE X. & CHAPUIS J.L., 2007 - Les mammifères terrestres non volants
740	des Antilles françaises et l'introduction récente d'un écureuil. <i>Revue d'écologie (Terre &amp; Vie)</i> , <b>62</b> ,
741	295-314.
742	
743	
744	MCFARLANE D.A. & MACPHEE R.D.E., 1993 - Amblyrhiza and the vertebrate paleontology of
745 746	anguillean caves. Bol. Soc. Venezolana Espel., 27, 33-38.
747	
747 748	NEWSOM L.A. & WING E.S., 2004 - On Land and Sea: Native American Uses of Biological Resources in
748 749	the West Indies. University of Alabama Press, United States of America, 344 p.
749 750	the west males. Oniversity of Alabama Press, Onited States of America, 544 p.
751	
752	NOKKERT M., 1999 - Faunal exploitation. In C. L. Hofman et M. L. P. Hoogland (eds.), Archaeological
753	investigations on St. Martin (Lesser Antilles). The sites of Norman Estate, Anse de Pères, and Hope
754	<i>Estate, with a contribution to the 'La Hueca Problem'</i> . <b>4</b> . ASLU, Leiden, 51-60.
755	Estate, whith a contribution to the Earnacea Hobient . 4. ASEO, Leiden, ST 00.
756	
757	OLSON S.L. & JAMES H.F., 1982 - Fossil Birds from the Hawaiian Islands: Evidence for Wholesale
758	Extinction by Man before Western Contact. Science, 217, (4560), 633-635,

759 760	10.1126/science.217.4560.633.
761 762 763 764 765	<b>PILSBRY H.A., 1904</b> - Manual of Conchology, Structural and Systematic. Second Series: Pulmonata, Vol. 16 - Urocoptidae, Achatinidae. Philadelphia, USA, Academy of Natural Sciences of Philadelphia, 329 p.
766 767 768 769 770	<b>PILSBRY H.A., 1907</b> - Manual of Conchology, Structural and Systematic. Second Series: Pulmonata, Vol. 19 - Oleacinidae-Ferussacidae. Philadelphia, USA, Academy of Natural Sciences of Philadelphia, 366 p.
771 772 773 774 775	<b>PILSBRY H.A., 1916</b> - Manual of Conchology, Structural and Systematic. Second Series: Pulmonata, Vol. 24 - Pupillidae (Gastricoptinae). Philadelphia, USA, Academy of Natural Sciences of Philadelphia, 380 p.
776 777 778 779	<b>PILSBRY H.A., 1948</b> - <i>Land Mollusca of North America (North of Mexico)</i> . Academy of Natural Sciences of Philadelphia, Philadelphia, 1113 p.
780 781 782 783	<b>POWELL R. &amp; HENDERSON R.W., 2012</b> - Island list of West Indian amphibians and reptiles. <i>Bulletin of Florida Museum of Natural History</i> , <b>51</b> , (2), 85-166.
784 785 786 787	<b>PREGILL G.K., STEADMAN D.W., OLSON S.L. &amp; GRADY F.V., 1988</b> - Late Holocene fossil vertebrates from Burma Quarry, Antigua, Lesser Antilles. <i>Smithsonian contribution to zoology</i> , <b>463</b> , 1-27.
788 789 790 791 792	<b>PREGILL G.K., STEADMAN D.W. &amp; WATTERS D.R., 1994</b> - Late Quaternary vertebrate faunas of the Lesser Antilles: historical components of Caribbean biogeography. <i>Bulletin of Carnegie Museum of Natural History</i> , <b>30</b> , 1-51.
793 794 795 796	<b>QUESTEL K., 2017</b> - Les escargots terrestres de Saint-Barthélemy. <i>Le bulletin de l'Agence Territoriale de l'Environnement de Saint-Barthélemy</i> , <b>1</b> , 10-13.
797 798 799 800 801	<b>REIG O.A., 1977</b> - A Proposed Unified Nomenclature for the Enamelled Components of the Molar Teeth of the Cricetidae (Rodentia). <i>Journal of Zoology</i> , <b>181</b> , (2), 227-241, 10.1111/j.1469-7998.1977.tb03238.x.

802 803 804 805 806	<b>RICKLEFS R.E. &amp; LOVETTE I.J., 1999</b> - The Roles of Island Area per Se and Habitat Diversity in the Species–Area Relationships of Four Lesser Antillean Faunal Groups. <i>Journal of Animal Ecology</i> , <b>68</b> , (6), 1142-1160, 10.1046/j.1365-2656.1999.00358.x.
807 808 809 810	<b>ROUGHGARDEN J., 1995</b> - <i>Anolis lizards of the Caribbean: ecology, evolution and plate tectonics.</i> Oxford Press, New-York, USA, 200 p.
811 812 813 814	SHUTTLEWORTH R.J., 1854 - Beiträge zur näheren Kenntniss der Land- und Süsswasser-Mollusken der Insel Portorico. <i>Mittheilungen der Naturforschenden Gesellschaft in Bern</i> , 310-330, 33-56.
815 816 817 818	<b>STEADMAN D.W., 1995</b> - Prehistoric Extinctions of Pacific Island Birds: Biodiversity Meets Zooarchaeology. <i>Science</i> , <b>267</b> , (5201), 1123-1131, 10.1126/science.267.5201.1123.
819 820 821 822 823	<b>STEADMAN D.W., PREGILL G.K. &amp; OLSON S.L., 1984</b> - Fossil Vertebrates from Antigua, Lesser Antilles: Evidence for Late Holocene Human-Caused Extinctions in the West Indies. <i>Proceedings of the</i> <i>National Academy of Sciences of the United States of America</i> , <b>81</b> , 4448-4451.
824 825 826 827 828 829	<b>STOETZEL E., ROYER A., COCHARD D. &amp; LENOBLE A., 2016</b> - Late Quaternary changes in bat palaeobiodiversity and palaeobiogeography under climatic and anthropogenic pressure: new insights from Marie-Galante, Lesser Antilles. <i>Quaternary Science Reviews</i> , <b>143</b> , 150-174, 10.1016/j.quascirev.2016.05.013.
830 831 832 833 834 835	<b>TURVEY S.T., WEKSLER M., MORRIS E.L. &amp; NOKKERT M., 2010</b> - Taxonomy, Phylogeny, and Diversity of the Extinct Lesser Antillean Rice Rats (Sigmodontinae: Oryzomyini), with Description of a New Genus and Species. <i>Zoological Journal of the Linnean Society</i> , <b>160</b> , (4), 748-772, 10.1111/j.1096-3642.2009.00628.x.
836 837 838 839	WATTERS D.R., REITZ E.J., STEADMAN D.W. & PREGILL G.K., 1984 - Vertebrates from archaeological sites on Barbuda, West Indies. <i>Annals of Carnegie Museum</i> , 53, 383-412.
840 841 842 843	WATTERS T.G., 2014 - A Preliminary Review of the Annulariidae (Gastropoda: Littorinoidea) of the Lesser Antilles. <i>The Nautilus</i> , <b>128</b> , (3), 65-90.

**YOKOYAMA M., 2013** - The incomplete guide to the wildlife of Saint-Martin. 2013.

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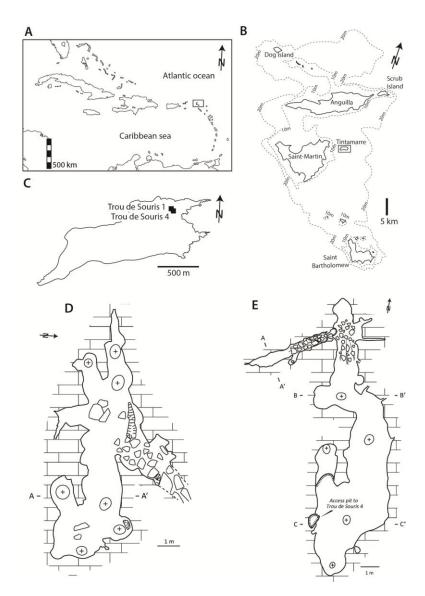




Fig. 1: Maps. (A) Map of the West Indies with the location of the Anguilla island bank. (B)
Map of the Anguilla island bank with the location of Tintamarre Island. C) Map of Tintamarre
Island with the location of the *Trou de Souris* 1 and 4 sites. (D) Map of *Trou de Souris* 1. (E)
Map of *Trou de Souris* 4.

Fig. 1: Cartes et plans. (A) Carte des Antilles avec la localisation du banc d'Anguilla. (B)

854 Carte du banc d'Anguilla avec la localisation de l'île de Tintamarre. (C) Carte de l'île de

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855 Tintamarre avec la localisation des sites de Trou de Souris 1 et 4. (D) Plan du site de Trou

*de Souris 1. (E) Plan du site de Trou de Souris 4.* 

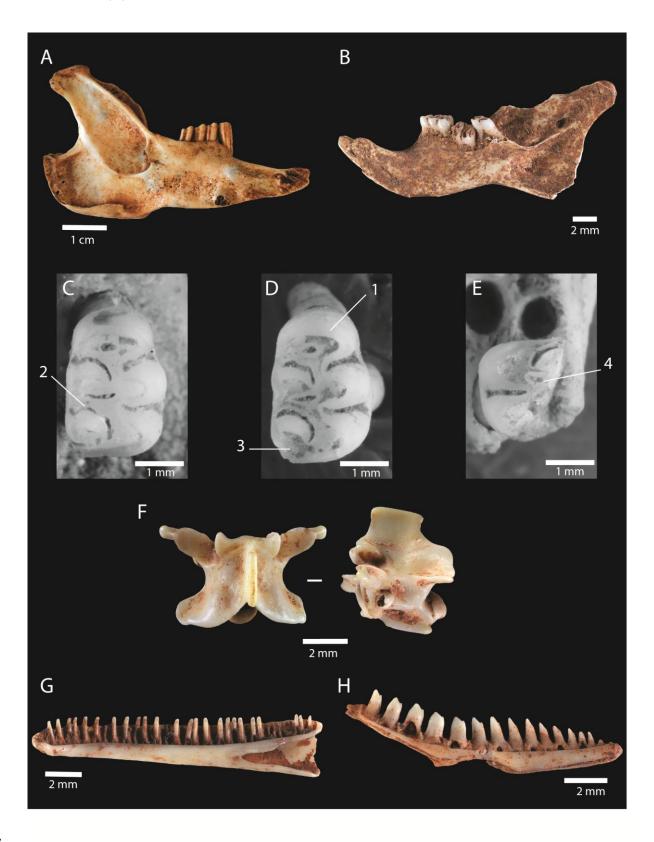
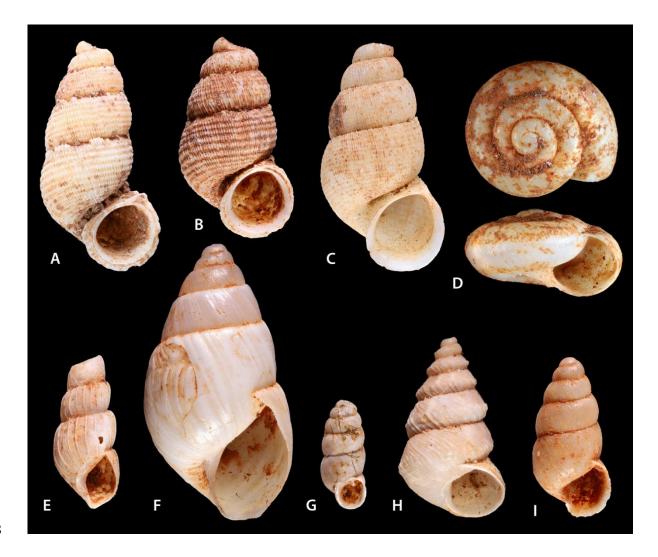


Fig. 2: Some of the most characteristic vertebrate remains identified from the sites of 858 859 Trou de Souris 1 and 4. (A) Lingual view of a left mandible of Oryctolagus cuniculus. (B) Lingual view of a right mandible of Rattus rattus. (C) Occlusal view of a right M1 of 860 Pennatomys nivalis. (D) Occlusal view of a right M1 of Pennatomys nivalis. (E) Occlusal 861 view of a right M2 of Pennatomys nivalis. (F) Trunk vertebra of Alsophis sp. in dorsal view 862 (left) and lateral view (right). (G) Lingual view of a right dentary of *Thecadactylus* sp. (H) 863 Lingual view of a left dentary of Pholidoscelis sp. Dental structures: 1: Anteromedian flexus 864 absent. 2: well-developed mesoloph. 3: Posteroflexus as a notch at the posterior margin of the 865 metacone, 4: mesoflexus present as a single internal fossette. Terminology according to Reig 866 867 (1977).

Fig. 2 : Quelques-uns des ossements de vertébrés les plus caractéristiques identifiés dans les 868 sites de Trou de Souris 1 et 4. (A) Mandibule gauche d'Oryctolagus cuniculus en vue 869 linguale. (B) Mandibule droite de Rattus rattus en vue linguale. (C) Vue occlusale d'une MI 870 droite de Pennatomys nivalis. (D) Vue occlusale d'une M1 droite de Pennatomys nivalis. (E) 871 Vue occlusale d'une M2 droite de Pennatomys nivalis. (F) Vertèbre troncale d'Alsophis sp. 872 en vue dorsale (gauche) et vue latérale (droite). (G) Dentaire droit de Thecadactylus sp. en 873 vue linguale. (H) Dentaire gauche de Pholidoscelis sp. en vue linguale. Structures dentaires: 874 1: absence du flexus antero-médian. 2: Mésolophe bien développé. 3: Posteroflexus formant 875 une encoche sur la marge postérieure du métacone, 4: Mésoflexus présent sous la forme 876 d'une fossette interne unique. Terminologie suivant Reig (1977). 877



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Fig. 3: Lateral views of some of the terrestrial snail shells collected on Tintamarre 879 Island. Sampling location in brackets. (A) Diplopoma crenulatum (SXM-009), elongate conic 880 morph, height = 11.9 mm. (B) Diplopoma crenulatum (TS4), short conic morph, height = 8.4 881 mm. (C) Chondropoma pupiforme (TS1), height = 11.5 mm. (D) Hyalosagda subaquila 882 (TS4), diameter = 4.4 mm. (E) Melaniella gracillima (SXM\_009), height = 3.3 mm; F: 883 Bulimulus lehmani (TS4), height = 12.8 mm. (G) Gastrocopta barbadensis (TS4), height= 2.3 884 mm. (H) Pseudopineria viequensis (SXM\_009), height = 4.9 mm. (I) Pupoides albilabris 885 (TS4), height = 3.8 mm. 886

Fig. 3 : Vues latérales de certaines des coquilles d'escargots terrestres collectées sur l'îlet
Tintamarre. La station de collecte est indiquée entre parenthèses. (A) Diplopoma crenulatum,

889	$morphe allong \acute{e} conique (SXM_009), hauteur = 11,9 mm. (B) Diplopoma crenulatum, morphe$
890	conique trapus (TS4), hauteur = $8,4$ mm. (C) Chondropoma pupiforme (TS1), hauteur = $11,5$
891	mm. (D) Hyalosagda subaquila (TS4), diamètre= 4,4 mm. (E) Melaniella gracillima (SXM-
892	009), hauteur = $3,3 \text{ mm.}$ (F) : Bulimulus lehmani (TS4), hauteur = $12,8 \text{ mm.}$ (G) Gastrocopta
893	barbadensis (TS4), hauteur= 2,3 mm. (H) Pseudopineria viequensis (SXM-009), hauteur =

894 4,9 mm. (I) Pupoides albilabris (TS4), hauteur = 3,8 mm.

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			Trou de Souris 1	Trou de Souris 4
Mammalia	Rodentia	Rattus rattus	1	
		Pennatomys nivalis	3	1
		Mus musculus	6	3
		Dasyprocta leporina	1	
		Unidentified	76	25
	Lagomorpha	Oryctolagus cuniculus	22	6
	Artiodactyla	Caprinae	11	
	Carnivora	Felis catus	1	
	Chiroptera	Phyllostomidae	1	
	Unidentified	Unidentified	6	3
Squamata	Serpentes	Alsophis sp.	85	6
-		Colubridae ind.	31	3
	Lacertilia	Anolis sp.	56	34
		Thecadactylus sp.	24	38
		Pholidoscelis sp.	10	7
	Unidentified	Unidentified	5	
Testudines		cf. Chelonoidis carbonaria	4	
Aves	Columbiformes	Columbina passerina	3	
		cf. Columbina passerina	2	
		Zenaida cf. aurita		1
	Passeriformes	Margarops fuscatus	1	
	Unidentified	Unidentified	1	1
Amphibia	Anura	Eleutherodactylus sp.	1	1
Verte brata		Unidentified	38	2
		Tota	389	131

#### 896

897 Tab. 1: Numbers of vertebrate bone remains collected and identified from the sites of

898 Trou de Souris 1 and 4.

### 899 Tab. 1: Comptage des ossements de vertébrés collectés et identifiés dans les sites de Trou de

900 *Souris 1 et 4.* 

901

		Species	Trou de Souris			Outdoor localities				
Order	Family		TS1	TS4	009	012	013	014	015	016
Littorinimorpha	Annulariidae									
		Chondropoma pupiforme	+	+						
		Diplopoma crenulatum 1	+	+	+	+	+			
Stylommatophora	Sagdidae									
		Hyalosagda subaquilla		+	+					
	Oleacinidae									
		Melaniella gracillima			+					
	Bulimulidae									
		Bulimulus lehmani		+					+	
		gen et sp. indet		+						
	Gastrocoptidae									
		Gastrocopta barbadensis *1			+			+		+
		Gastrocopta pellucida						+		
		Gastrocopta polyptyx *								
		Gastrocopta servilis * 1						+		
	Pupillidae									
		Pupoides albilabris * 1		+						
	Urocoptidae									
		Pseudopineria viequensis 1	+	+	+		+		+	+
	Achatinidae									
		Allopeas micra 1								
		* : reconnu par Haas (1960)								
		1 : reconnu par Hovestadt et Ne	ckheim (2	2020)						

Tab. 2: Presence versus absence data of the identified species of terrestrial snails at the
two sites of Trou de Souris 1 and 4 and at several outdoor localities. Species with an
asterisk are those previously found on Tintamarre by Haas (1960), and those with a dagger by
Hovestadt and Neckheim (2020).

<sup>Tab. 2 : Données d'occurrence des escargots terrestres dans les deux sites de Trou de Souris
1 et 4 ainsi que dans les lieux de prélèvement en plein-air. Les espèces marquées d'un
astérisque sont celle mentionnées précédemment sur Tintamarre par Haas (1960), et celle
marquée d'un obèle les espèces listées par Hovestadt et Neckheim (2020).</sup>