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

Corentin Bochaton^{1,2}, David Cochard¹, Monica Gala¹, Julien Chalifour³ & Arnaud Lenoble¹

¹ - PACEA – UMR CNRS 5199, Université de Bordeaux, 33 615 Pessac, France. *Courriel* :
corentin.bochaton@u-bordeaux.fr; david.cochard@u-bordeaux.fr; monica.gala@u-bordeaux.fr; arnaud.lenoble@u-bordeaux.fr.

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

³ - Réserve Naturelle de Saint Martin (AGRNSM), 11 et 13 Rue Barbuda, Hope Estate,
97 150, Saint Martin.

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; palaeontology; 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 îles 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**

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

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

51 Tintamarre is a small island of 0.8 km² entirely composed of limestone (Dugain *et al.*, 1989).
52 This island is part of the Anguilla bank, mainly composed of the islands of St. Martin, Saint-
53 Barthelemy, and Anguilla that are currently separated by areas of sea less than 30m deep, and
54 during the Late Pleistocene formed a single island (Christman, 1953). Tintamarre is nearly
55 flat with a maximum elevation of 30m and is particularly dry due to a combination of low
56 precipitation and a porous limestone substrate. The vegetation of Tintamarre includes the
57 remnant of a dry deciduous forest with numerous xerophytes and succulent plant species, part
58 of a semi-deciduous forest on the plateau with lignum vitae (*Gaiacum officinale*) and water
59 mampoo (*Pisonia subcordata*), and finally salt-tolerant trees like manchineel (*Hippomane*
60 *mancinella*) and seagrape (*Coccoloba uvifera*) near the lagoons and beaches (Impact
61 Mer, 2020). Nothing is currently known about the past biodiversity of Tintamarre but its
62 modern faunal diversity is extremely poor. Tintamarre is currently occupied only by around
63 33 vertebrate species, and with no more than seven species of terrestrial mollusks discovered
64 by the collecting missions carried out in the second part of the twentieth century (Hovestadt &
65 Neckheim, 2020). Initially only four taxa in the families Gastropodidae and Pupillidae were
66 known from the material collected in 1949 by A. Hummelinck (Hummelinck, 1981) and
67 published by Haas (1960), before three new taxa were added after the recent review of the
68 collections made in the 1970s by Hummelinck (Hovestadt & Neckheim, 2020). Mammals are
69 currently represented by at least three species: goats (*Capra hircus*), black rats (*Rattus rattus*),
70 and house mice (*Mus musculus*) (Brown, 2008, pers. obs.). Brown rats (*Rattus norvegicus*)
71 may have once been present but recent trapping campaigns have demonstrated they are not
72 currently found on Tintamarre (Lorvelec *et al.*, 2013 ; Lorvelec *et al.*, 2017). Mongooses and
73 cats are absent from the Island. In respect to reptiles, the Tintamarre islet is currently occupied
74 by five species of lizards: the Anguilla Bank ameiva (*Pholidoscelis plei*), the Anguilla Bank
75 tree anole (*Anolis gingivinus*), the Anguilla Bank skink (*Spondylurus powelli*), the

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

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

101 1947 (Casius, 2005). At that time the island was only occupied by some employees of the
102 company, and is since free of all permanent human occupation although tourists still frequent
103 the beach. There is also some sparse evidence of an occupation of the island during the pre-
104 Columbian era, but this needs to be described with greater precision (Hénocq, 2019). The
105 impact of each different phases of occupation has remained until now completely unknown,
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
108 of Tintamarre Island based on the study of subfossil remains collected from two fossil-bearing
109 cave deposits on the island.

110 **2 - MATERIALS AND METHODS**

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

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

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

155 **3 - RESULTS**

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

159 3.1 - VERTEBRATE BONE REMAINS (TAB. 1)

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

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

182 Among the other mammal taxa, 28 remains were identified as *Oryctolagus cuniculus*
183 (Linnaeus, 1758) including a complete mandible (fig. 2-A). Some remains of Caprinae
184 (phalanx and petrosal bones) were also identified but no diagnostic elements were present that
185 would have allowed a specific identification as either *Capra* or *Ovis*. An unidentified
186 Phyllostomid bat was represented by a single clavicle, and a cat canine (*Felis catus*;
187 (Linnaeus, 1758)) and a probable lower incisor of Agouti (*Dasyprocta leporina*; Linnaeus,
188 1758) was also present.

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

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

218 Nine bird remains representing two species of Columbidae (*Columbina passerina* (Linnaeus,
219 1758), *Zenaida* cf. *aurita* (Temminck, 1809), and the passeriform *Margarops fuscatus*
220 (Vieillot, 1808) have been collected across the two sites (Tab. 1). These bones were identified
221 from their morphological similarity to modern specimens. *Zenaida* cf. *aurita* is represented by
222 a single fragment of ulna and was identified from the morphology of the *condylus dorsalis*

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

226 3.2 - TERRESTRIAL SNAIL SHELLS (TAB. 2)

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

231 Annulariidae shells were collected at the majority of collection points but were only
232 represented by old or fossil (fully mineralized) specimens. Two species are represented; most
233 specimens are of a medium to small-size, ranging from an elongate conic shape (fig. 3-A) to a
234 short conic shape (fig. 3-B), both displaying equally developed spiral rounded cords and axial
235 erected lamellae fusing to form tufts in the sutures of the whorls. These features agree with
236 identification as *Diplopoma crenulatum* (Potiez & Michaud, 1835) (see also criteria in
237 Watters, 2014), the elongate morph being similar to the specimen from St. Martin illustrated
238 by Watters (*op. cit.* fig. 100). The short conic morph is characterized by a smaller length,
239 lower number of whorls (up to 4 ½), more prominent spiral cords, and very developed sutural
240 tufts that are frequently broken off. All these characteristics make this morph similar to the
241 *Diplopoma sulculosum* species (Pfeiffer, 1852) known from the neighboring island of
242 Anguilla, although *D. sulculosum* has more pronounced features (see criteria in Watters,
243 2014). This short morph is also indistinguishable from the St. Barth specimens assigned to *D.*
244 *crenulatum* by Questel (2017) and *D. sulculosum* by Hovestadt and Neckheim (2020). This
245 morph and Tintamarre's general population of *D. crenulatum* therefore present characteristics
246 that are intermediary between *D. crenulatum* and *D. sulculosum*, which raises taxonomic

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

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

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

285 **4 - DISCUSSION**

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

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

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

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

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

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

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

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

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

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

397 The only Tintamarre species absent from St. Martin is *Bulimulus lehmani*, a species present
398 on the island of Anguilla, while the genus *Bulimulus* is currently represented on St Martin by
399 *Bulimulus diaphanus* and *B. guadalupensis* (Breure, 1974). *Bulimulus lehmani* was formerly
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
402 the systematic surveys carried out during the last few decades (Hovestadt &
403 Neckheim, 2020). In this study, we demonstrate the past presence of *B. lehmani* on
404 Tintamarre but this species is only represented by few old shells. The status of this species on
405 the island still has to be demonstrated and it could have been unintentionally introduced from
406 Anguilla during historical times as many Tintamarre workers were Anguillan inhabitants.

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

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

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

452 **5 - CONCLUSION**

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

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

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

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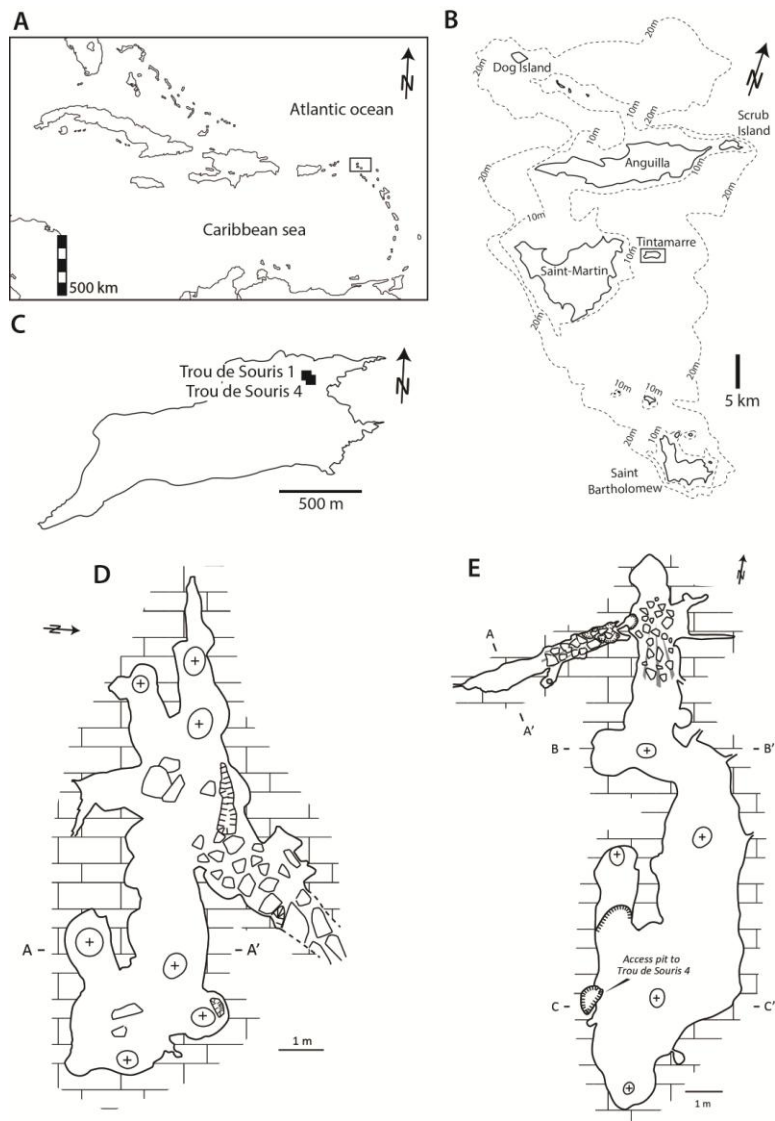
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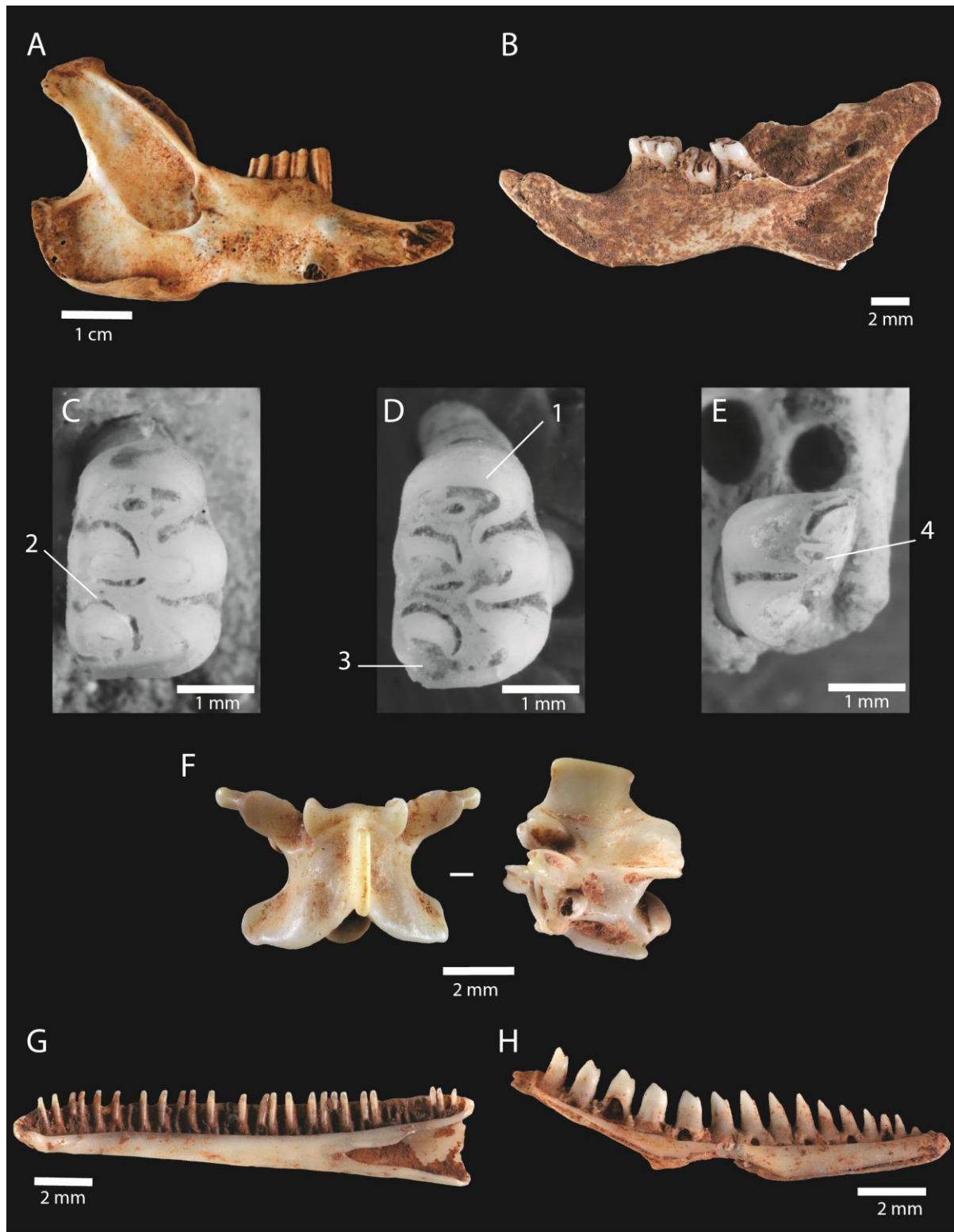
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849 **Fig. 1: Maps.** (A) Map of the West Indies with the location of the Anguilla island bank. (B)
850 Map of the Anguilla island bank with the location of Tintamarre Island. (C) Map of Tintamarre
851 Island with the location of the *Trou de Souris*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

853 **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*

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

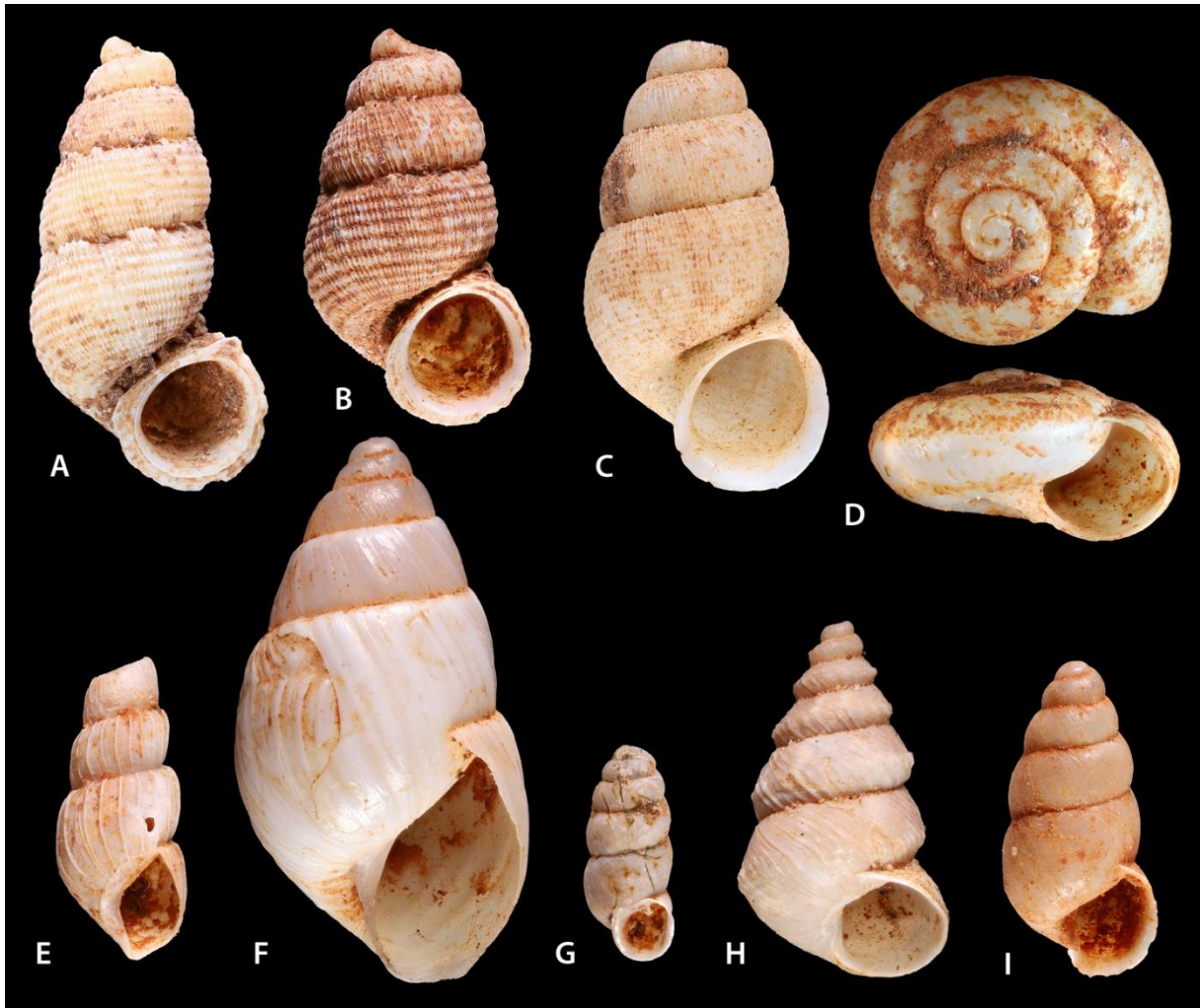
856 *de Souris 1. (E) Plan du site de Trou de Souris 4.*



857

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

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



878

879 **Fig. 3: Lateral views of some of the terrestrial snail shells collected on Tintamarre**
 880 **Island.** Sampling location in brackets. (A) *Diplopoma crenulatum* (SXM-009), elongate conic
 881 morph, height = 11.9 mm. (B) *Diplopoma crenulatum* (TS4), short conic morph, height = 8.4
 882 mm. (C) *Chondropoma pupiforme* (TS1), height = 11.5 mm. (D) *Hyalosagda subaquila*
 883 (TS4), diameter = 4.4 mm. (E) *Melaniella gracillima* (SXM_009), height = 3.3 mm; F:
 884 *Bulimulus lehmani* (TS4), height = 12.8 mm. (G) *Gastrocopta barbadensis* (TS4), height= 2.3
 885 mm. (H) *Pseudopineria viequensis* (SXM_009), height = 4.9 mm. (I) *Pupoides albilabris*
 886 (TS4), height = 3.8 mm.

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

889 *morphe allongé 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 mm. (F) : Bulimulus lehmani (TS4), hauteur = 12,8 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.*

895

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

Order	Family	Species	Trou de Souris		Outdoor localities						
			TS1	TS4	009	012	013	014	015	016	
Littorinimorpha	Annulariidae	<i>Chondropoma pupiforme</i>	+	+							
		<i>Diplopoma crenulatum</i> †	+	+	+	+	+				
Stylommatophora	Sagdidae	<i>Hyalosagda subaquilla</i>		+	+						
		Oleacinidae	<i>Melaniella gracillima</i>			+					
	Bulimulidae		<i>Bulimulus lehmani</i>		+						+
		<i>gen et sp. indet</i>		+							
	Gastrocoptidae	<i>Gastrocopta barbadensis</i> * †				+			+		+
		<i>Gastrocopta pellucida</i>							+		
		<i>Gastrocopta polyptyx</i> *									
		<i>Gastrocopta servilis</i> * †							+		
	Pupillidae	<i>Pupoides albilabris</i> * †		+							
	Urocoptidae	<i>Pseudopineria viequensis</i> †	+	+	+			+		+	+
	Achatinidae	<i>Allopeas micra</i> †									

* : reconnu par Haas (1960)

† : reconnu par Hovestadt et Neckheim (2020)

901

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

906 *Tab. 2 : Données d'occurrence des escargots terrestres dans les deux sites de Trou de Souris*
 907 *1 et 4 ainsi que dans les lieux de prélèvement en plein-air. Les espèces marquées d'un*
 908 *astérisque sont celle mentionnées précédemment sur Tintamarre par Haas (1960), et celle*
 909 *marquée d'un obèle les espèces listées par Hovestadt et Neckheim (2020).*