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L'herpétofaune fossile et subfossile de la grotte Cadet 2 (Marie-Galante, Archipel de la Guadeloupe, P.-A. F.) : Evolution d'une herpétofaune insulaire depuis le Pléistocène supérieur

Fossil and subfossil herpetofauna from Cadet 2 Cave (Marie-Galante, Guadeloupe Islands, F. W. I.): Evolution of an insular herpetofauna since the Late Pleistocene

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4 Abstract
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6 This study deals with the herpetofaunal fossil and subfossil remains from the Cadet 2 site (Marie-
7 Galante, Guadeloupean Archipelago). This study provides new data concerning the herpetofaunal
8 community since the Late Pleistocene by revealing the early local occurrence of some taxa
9 (*Eleutherodactylus* sp., cf. *Sphaerodactylus* sp., *Ameiva* sp., cf. *Capitellum mariagalantae*, *Anolis* cf.
10 *ferreus*, cf. *Antillotyphlops* sp., cf. *Alsophis* sp. and Colubroidea sp. 1) and possible Pleistocene extinctions
11 (*Boa* sp. and Colubroidea sp. 2). Moreover, the first metric data for fossil Marie-Galante anoles show
12 clear size stability throughout time. As regards the evolution of the island herpetofaunal biodiversity, our
13 work points to the long-term stability of the fauna before human colonization and subsequently to the
14 marked impact of human-caused environmental disturbances during colonial but also Pre-Columbian
15 periods.
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21 Key words: West-Indies, Herpetofauna, Paleontology, Biodiversity, Extinction, Guadeloupe islands, faunal
22 turnover.
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27 **Résumé**
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29 Nous étudions ici le matériel herpétofaunistique provenant du site de Cadet 2 situé sur l'île de Marie-
30 Galante dans l'Archipel de la Guadeloupe. L'analyse de ces restes apporte des données inédites
31 concernant le peuplement herpétologique de l'île depuis le Pléistocène supérieur. Elle met en évidence
32 la présence ancienne de certains taxons sur l'île (*Eleutherodactylus* sp., cf. *Sphaerodactylus* sp., *Ameiva*
33 sp., cf. *Capitellum mariagalantae*, *Anolis* cf. *ferreus*, cf. *Antillotyphlops* sp., cf. *Alsophis* sp. et Colubroidea
34 sp. 1). Elle montre aussi de possibles extinctions datant du Pléistocène (*Boa* sp. et Colubroidea sp. 2).
35 Nos premiers résultats obtenus sur les faibles variations de la taille des anoles fossiles de Marie-Galante
36 démontrent la grande stabilité des peuplements au cours du temps. Ce travail met en avant la stabilité
37 de l'herpétofaune de l'île durant les périodes précédant l'arrivée de l'homme puis les modifications
38 considérables qui suivent son installation pendant les périodes précolombiennes puis modernes.
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43 Mots-clés: Antilles, Herpétofaune, Paléontologie, Biodiversité, Extinction, Guadeloupe, remplacement de
44 faune.
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49 **Introduction**
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51 The biogeography of the Greater and Lesser Antilles herpetofauna has been the subject of several
52 publications during the past decades (Hedges, 1996; Hedges, 2006; Lescure, 1987; Lescure *et al.*, 1991).
53 Thus, the present-day composition and distribution of the herpetofauna on the Caribbean Islands is well
54 known (Henderson and Powell, 2009; Powell and Henderson, 2012). In the same way, the modern
55 herpetofauna on the Guadeloupe Islands is well documented and has recently been the subject of a
56 monograph (Breuil, 2002). In contrast, the fossil and subfossil herpetofauna is poorly known, in particular
57 in the Lesser Antilles (Pregill and Olson, 1981; Pregill *et al.*, 1988; Pregill *et al.*, 1994). Many questions
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4 remain unresolved as regards the past Guadeloupean herpetofaunal community and in spite of several
5 studies focusing on archaeological fauna (Grouard, 2001, 2003, 2007, 2010), pre-anthropoc fossil data for
6 reptiles and amphibians have remained scant since the pioneering work of Pregill (1994). In addition, the
7 impact of human populations on herpetological communities during Amerindian and colonial periods is
8 sparsely documented although some works have attempted to tackle this question (Pregill, 1986;
9 Steadman *et al.*, 1984).
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13 The recent exploration and excavation of fossil-bearing deposits in Guadeloupe and Marie-Galante
14 considerably improve our knowledge of past Guadeloupean biodiversity (Grouard *et al.*, 2014; Lenoble *et*
15 *al.*, 2009; Stouvenot *et al.*, 2014). The present study focuses on reptile and amphibian remains collected
16 from one of these sites, the Cadet 2 Cave, which lies on the southeastern coast of Marie-Galante, and
17 documents the composition and evolution of the Marie-Galante herpetofauna over the past thirty
18 thousand years.
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22 Marie-Galante Island and site description

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24 Marie-Galante (61.223358 W; 15.893134 N) (Fig. 1) is a small, low-lying limestone island of
25 approximately 158 km² (maximum altitude = 202 m). It probably emerged during the late Calabrian
26 about 800,000 years ago (Münch *et al.*, 2013). Six squamate species occur nowadays on the island: three
27 of them are considered to be native species (*Anolis ferreus*, *Sphaerodactylus fantasticus anidrotus* and
28 *Thecadactylus rapicauda*) and three others as recently introduced species (*Iguana iguana*,
29 *Gymnophthalmus underwoodi* and *Hemidactylus mabouia*). There are also three species of frogs, one
30 native (*Eleutherodactylus martinicensis*) and two allochthonous (*Eleutherodactylus johnstonei* and *Scinax*
31 *cf. x-signatus*). Several other currently extinct taxa have been mentioned by naturalists over the past
32 centuries, including three squamates, the scincid *Capitellum mariagalantae* and two snakes (*Alsophis*
33 *antillensis* and *Liophis juliae*) (Breuil, 2002). In addition the genus *Iguana* have been mention in Marie-
34 Galante archaeological deposits dated from 200 to 1000 AD (Grouard, 2001; Bochaton, com. pers.). The
35 Cadet 3 fossil deposit (Stouvenot *et al.*, 2014) containing layers dated from 13 800 BC to modern time
36 provides evidence of three additional extinct taxa, hitherto never mentioned on the island (*Boa* sp.,
37 *Ameiva* sp. and *Leiocephalus cuneus*). *Ameiva* was previously thought to have been present on Marie-
38 Galante during the past by Breuil (2002), but clear evidence was lacking.
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46 Cadet 2 is a flank margin cave (Lenoble *et al.*, 2009) opening onto the cliff of the Capesterre terrace near
47 the Cadet 3 site, about 250 m from the coast (Fig. 1). The site was first excavated by P. Courtaud from
48 2004 to 2007 in order to record Amerindian burials (Courtaud, 2011; Courtaud *et al.*, 2005). Due to the
49 paleontological potential of the site (Lenoble *et al.*, 2009) another excavation was subsequently directed
50 by S. Grouard in 2010 to investigate the pre-anthropoc layers and to collect the vertebrate remains. This
51 last excavation focused on two loci described below.
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55 The first locus (Fig. 1) is located in the deepest part of the cave. It measures one square meter and
56 reaches a depth of 1.4 meters. This locus contains a large part of the cave infilling. Above a basal
57 accumulation of sands rich in seashells and land crab fragments (U5-D), the deposits correspond to a
58 succession of bedded silt, divided into three subunits following the sedimentary structure (U5-C to U5-
59 A). The organic silt fraction was radiocarbon dated at the *Centre de datation par radiocarbone de Lyon*
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4 (France). The dates range between 34,229 – 31,888 cal. BC and 11,909 – 11,530 cal. BC (Ref.: Ly 8,496-
5 8,492) (Fig. 1). Above these levels, lies layer U4-U4', corresponding to an undated non-excavated
6 archaeological level, probably of Holocene age. An archaeological pit was identified in layer U4 (ST 500
7 see Fig. 1). This structure is contemporaneous with the Amerindian occupation of the cavity, estimated
8 to date from the 14th century AD (Courtaud, 2011; Courtaud *et al.*, 2005).
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12 The second locus was excavated over half a square meter and divided into six levels. The radiocarbon
13 dating of a charcoal from level U5-b at the Erlangen laboratory (Germany) yielded ages of 28,413 –
14 27,425 cal. B.C. (Ref.: Erl 14,011). On the basis of the characteristics of the sediment facies, the
15 stratigraphic units of this locus were correlated with layers U5-C and U5-B from the first locus, and are
16 thus considered to be of Pleistocene age.
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19 The whole assemblage is made up of 131,571 osteological remains, including 57,468 (48 %) reptile and
20 amphibian remains collected in all the layers except U5-D which contained only few very fragmented
21 bones.
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26 **Material and Methods**

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29 The sediment samples from the site were washed with water using a 0.5 mm sieve mesh. The
30 osteological remains were collected with a binocular scope (Nikon SMZ1000).
31

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33 The osteological collections used for the identification of the remains (see Appendix 1) come from the
34 Muséum national d'Histoire naturelle (MNHN - Paris, France) (Comparative Anatomy –MNHN-ZA-AC-,
35 Reptile and Amphibians –MNHN-RA- and UMR 7209 “Archéozoologie et Archéobotanique” “Caraïbes” –
36 MNHN-UMR7209- collections) and UMR 5199 CNRS “PACEA” (PACEA - Bordeaux, France). We also
37 referred to several published osteological characteristics. In this study, we only describe the main
38 osteological features used for the identification of each taxon.
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42 These specimens come from the Muséum national d'Histoire naturelle (MNHN - Paris, France)
43 (Comparative Anatomy –MNHN-ZA-AC-, Reptile and Amphibians –MNHN-RA- and UMR 7209
44 “Archéozoologie et Archéobotanique” “Caraïbes” –MNHN-UMR7209- collections); UMR 5199 CNRS
45 “PACEA” (PACEA - Bordeaux, France) and Museum of Comparative Zoology (MCZ - Harvard, United-
46 States of America).
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49 The classifications employed here derive from several works concerning amphibians (Frost *et al.*, 2006;
50 Hedges *et al.*, 2008) and squamates (Conrad, 2008; Townsend *et al.*, 2011), including some on snakes
51 (Lee and Scanlon, 2002; Vidal *et al.*, 2010).
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54 The osteological features for frog identification are based on the synopsis by Hedges *et al.* (2008) and
55 Lynch (1971).
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58 The characteristics used to identify squamate cranial remains are those cited by Conrad (2008), Estes *et al.*
59 (1988) and Evans (2008). Post-cranial identification is based on the works of Etheridge (1967),
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4 Hoffstetter and Gasc (1969) and Lécuro (1968, 1969). Several other works were used to specifically
5 identify the Dactyloidae (Etheridge and De Queiroz, 1988; Etheridge, 1959; Frost and Etheridge, 1989;
6 Nicholson *et al.*, 2012; Poe, 1998, 2004), the Scincidae (Greer, 1970; Rao and Ramaswami, 1952) and the
7 Teidae (Kosma, 2004; Pujos *et al.*, 2009; Tedesco *et al.*, 1999).
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10 Snake vertebra identification is based on the works of Albino and Carlini (2008), Albino (2011), Lee and
11 Scanlon (2002) and Rage (1984).
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14 **Results**

15 Systematic account

16 Anura Duméril, 1806

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18 Eleutherodactylidae Lutz, 1954

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21 *Eleutherodactylus* sp. Duméril & Bibron, 1841 – 48,330 remains representing most anatomical parts.
22 Minimal Number of Individuals (MNI) = 4,405 based on the ilia.
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26 The eleutherodactylid frog attribution is based on the combined occurrence of the following features:
27 elongated maxillary bearing a high number of teeth (t.), without lateral dermal ornamentation but with a
28 thick maxillary shelf (M. s.) and short posterior process (M. p. pr) (Figs. 2 A-B); fused sphenethmoids;
29 unfused frontoparietals; fused prootic and frontoparietal; type 1 atlas articulation (*sensu* Lynch, 1971);
30 atlas and second vertebra neural arches not fully ossified; sacral vertebra with distally weakly expanded
31 and slightly posteriorly orientated sacral processes; elongated scapula with well-individualized acromial
32 and glenoid processes; ilium bearing a weak, medially incurved dorsal crest with a globular and laterally
33 placed superior tuberosity and distally fused tibia and fibular. In addition, the occurrence of vomerine
34 teeth is a feature encountered in the *Eleutherodactylus* genus (Hedges *et al.*, 2008) (Fig. 2 C).
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40 These osteological features, combined with present geographical distribution data, allow us to attribute
41 this frog to the genus *Eleutherodactylus*, and perhaps to a member of the *martincensis* series (*sensu*:
42 Hedges *et al.*, 2008). The only extant members of this genus occur in the Lesser Antilles. These remains
43 are present in all the Cadet 2 layers.
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46 Squamata Opperl, 1811

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48 Dactyloidae Fitzinger, 1843

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51 *Anolis* cf. *ferreus* (Cope, 1864) – 8,638 remains corresponding to most skeletal parts. MNI= 215 based on
52 the dentaries.
53

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55 Many of the observed features point towards an attribution of these bones to an iguanid whereas others
56 are typical of polychrotine iguanids (*sensu* Evans 2008 = Dactyloidae *sensu* Townsend *et al.*, 2011):
57 maxillary bearing a triangular facial process forming an anterodorsal plate (ad. p.) grooved by a furrow
58 (*canthus*) (c.) (Fig. 2 D); fused frontals without dorsal keel or pineal foramen and medially fused ventral
59 cranial crests (c. cr.) (Fig. 2 E); parietal bearing a Y-shaped crest and a pineal foramen on its anterior
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margin; jugal of angular type morphology; no pterygoidian teeth. In addition, the blunt extremity of the dentary posterior process (p. pr.) (Fig. 2 F) is characteristic of the *Anolis bimaculatus* series (Poe, 2004) which includes, among others, the north Lesser Antillean anoles. The maxillary and dentary tooth morphology is also characteristic of anoles; teeth are pleurodont and slightly labio-lingually flattened. The posterior teeth are tricuspid with a wider central cusp and two reduced anterior and posterior cusps. The anterior teeth tend to become more and more monocuspid.

The observed osteological features on all skeletal parts show that this taxon corresponds to one or more species of *Anolis* of the *bimaculatus* series (Poe, 2004). These remains are abundant in every Cadet 2 layer.

We estimated the fossil anole SVL size using the dental row length of each complete dentary by comparison with modern *Anolis ferreus* of known size. According to our estimations, fossil size ranges from 53 to 123 mm SVL, a range consistent with the present-day size of the Marie-Galante anole, *Anolis ferreus* (see Breuil, 2002). No significant size differences emerge between the Pleistocene and Holocene Cadet 2 layers (Wilcoxon-Mann-Whitney test; p. val >0.05) (Fig. 3 A). In addition, the clearly bimodal distribution of fossil size corresponds perfectly to female (73mm SVL maximum) and male (123mm SVL maximum) *Anolis ferreus* sizes (Fig. 3 B).

Sphaerodactylidae Underwood, 1954

cf. *Sphaerodactylus* sp. Wagler, 1830 – 1 femur. MNI=1

This single femur has been identified on the basis of its morphological proximity with *Sphaerodactylus fantasticus* and its reduced size (3 mm length), compared to all the other taxa described here. This taxon is only represented in the locus 2 Pleistocene layer.

Scincidae Gray, 1825

Mabuya (s. l.) sp. Fitzinger, 1826 (=cf. *Capitellum mariagalantae sensu* Hedges and Conn (2012)) – 2 maxillaries, 1 frontal, 2 parietals, 2 dentaries, 1 coronoid, 3 articular-surangulars, 10 dorsal vertebrae, 1 sacral vertebra, 5 caudal vertebrae, 3 pelvic girdles, 1 humerus, 3 femurs, 3 ulnas. MNI= 2

The following osteological characteristics allow us to identify this taxon as a Scincidae: maxillary bearing a bifid posterior process; fused frontals with weak intra-orbital constriction bearing slight ornamentation (or.) on its dorsal part and moderately strong, medially unconnected ventral cranial crests (c. cr.) (Fig. 4 A-B); fused parietals bearing slight dermal ornamentation, a central pineal foramen, long posterior processes but shorter than the parietal table and a deep posteromedial notch; dentary with a straight ventral margin, well-individualized posteroventral (pv. Pr.) and posterodorsal (pd. Pr.) processes and Meckel groove (M. g.) completely surrounded by bone on its anterior half (Figs. 4 C-D); articular, prearticular (pa.) and surangular (sa.) fused and retroarticular process (ra. pr.) rounded, well-developed and slightly inclined medially (Fig. 4 E); pleurodont, cylindrical and monocuspid teeth with rounded apex on maxillary and dentary bones.

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4 In addition, the small size of these remains and their morphological similarity with *Mabuya* (*sensu lato*)
5 lead us to attribute them to that genus, which is the only scincid genus traditionally recognized in the
6 Lesser Antilles. Following Hedges and Conn (2012), *Mabuya sensu lato* is currently divided into sixteen
7 genera but no osteological features have yet been proposed to differentiate them. Thus, relying
8 exclusively on geographical criteria, we suggest an attribution to the Marie-Galante skink, *Capitellum*
9 *mariagalantae sensu* Hedges and Conn (2012), (formerly *Mabuya mabuya*), mentioned for the last time
10 by Dunn (1935). These fossil remains occur from the oldest to the youngest Cadet 2 layers but are absent
11 from U5-B.
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15 16 Teiidae Gray, 1829

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18 *Ameiva* sp. (Meyer, 1795) – 2 premaxillaries, 8 maxillaries, 2 prefrontals, 4 frontals, 2 postorbitofrontals,
19 1 jugal, 2 pterygoids, 1 quadrate, 2 dentaries, 4 coronoids, 1 articular, 1 axis, 17 dorsal vertebrae, 3
20 second sacral vertebrae, 45 caudal vertebrae, 6 scapulocoracoids, 1 ischium, 3 humeri, 1 tibia and 2
21 femurs. MNI=4
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24 The main elements clearly show teiid squamate features: maxillary with long and high facial process (f.
25 p.) and without dermal ornamentation (Fig. 4 F); fused frontals with deep dorsolateral nasal bone
26 impressions (N. i.), a clearly visible dorsal ornamentation (or.) and low ventral cranial crests (c. cr.)
27 without anteroventral descendant process (Figs. 4 G-H); dentary Meckel groove (M. g.) fully open and
28 incurved dentary ventral margin (Fig. 4 I); articular angular process ventrally orientated; pleurodont
29 bicuspid or monocuspid teeth surrounded at their bases by dental cement and basally pierced by a
30 subcircular replacement pit; procoelous vertebrae with well-developed zygosphene that lacks an
31 anterior notch. In addition, the absence of pterygoidian teeth and the Meckel groove opening only
32 visible in lingual view are characteristic of *Ameiva* and the occurrence of monocuspid posterior teeth
33 with a rounded apex is a feature occurring in the Lesser Antillean *Ameiva* taxa (*A. fuscata*, *A. griswoldi*, *A.*
34 *plei* and *A. pluvianotata*) (Kosma, 2004; Pregill, 1984).
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40 These features allow us to identify this taxon as a member of the genus *Ameiva*, possibly comprised in
41 the Lesser Antillean *Ameiva* clade on the basis of its dental morphology. We estimate the size of this
42 squamate at around 150-200 mm SVL, which is similar to *A. cineracea* (from Basse-Terre), but smaller
43 than *A. major* (from Petite-Terre), the two previously described Guadeloupean ameivas considered to
44 have become extinct recently (Breuil, 2002) in Guadeloupe islands. A comparison with these taxa is
45 impossible as their skeletal morphology remains unknown. The ameiva remains are present from the
46 oldest to the youngest Cadet 2 layers but are absent from U5-B.
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50 51 Serpentes Linnaeus, 1758

52 53 Scolecophidia Cope, 1864

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55 Cf. *Antillotyphlops* Richmond, 1966 – 169 dorsal and caudal vertebrae.
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57 These vertebrae (Figs. 5 A-B) bear typical scolecophidian features. They are small with a centrum length
58 ranging from 0.9 to 1.65 mm. They bear a zygosphene/zygantrum articulation (zs.) but neither neural
59 spine nor hemal keel. The neural arch posterior margin is weakly notched. The prezygapophyseal
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4 processes (pz. pr.) are long, slender and anteriorly oriented. The cotyle is dorsoventrally flattened and
5 there are no paracotylar foramina. Synapophyses are simple and rounded.
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8 According to these features, these bone remains can be attributed to a scolecophidian snake. They could
9 be related to a member of the *Antillotyphlops* genus, the only genus occurring today in the north of the
10 Lesser Antilles (Hedges *et al.*, 2014). These typical vertebrae occur from Pleistocene to Holocene Cadet 2
11 layers but are absent from U5-C and U5-B.
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14 Alethinophidia Nopcsa, 1923

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16 Boidae Gray, 1825

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18 *Boa* sp. Linnaeus, 1758 – 16 dorsal vertebrae.
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21 These vertebrae (Figs. 5 C-E) bear all the *Boa* features: they are strongly built, are wider than they are
22 long and have a high neural arch and neural spine (ns.). The neural arch posterior margin is strongly
23 notched, the prezygapophyseal facets (prz. f.) are long and laterally oriented and the prezygapophyseal
24 processes (pz. pr.) are present but short. The zygosphene (zs.) is thick from an anterior view and its
25 anterior margin is more or less concave from a dorsal view. From a ventral view, there is a strong
26 precondylar constriction and the hemal keel (h. k.) is thin with a blunt ventral margin. A paracotylar
27 foramen (p. f.) is present on each cotyle side.
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31 These features allow us to attribute these vertebrae to a member of the genus *Boa*. The small size of the
32 vertebrae (centrum length ranging from 2.8 to 4.2 mm) suggests very small specimens with a SVL size of
33 around 80 cm. This raises the question of the juvenile character of these vertebrae, an hypothesis also
34 supported by the fact that vertebral cotyles and condyles are wider than high (Albino, 2011). Another
35 possibility could be membership in a dwarf specie but the material is too sparse to provide a clear
36 answer to this question. This taxon is only present in the Pleistocene U5-C and Locus 2 layers of Cadet 2.
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40 Colubroidea Opperl, 1811

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42 Cf. *Alsophis* sp. Fitzinger, 1843 - 155 dorsal and caudal vertebrae.
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45 These vertebrae (Figs. 5 F-H) are weakly built and are relatively more elongate than those of non-
46 colubroid Cadet 2 snakes. The centrum is longer than wide and has length ranges from 0.8 to 3.5 mm. In
47 dorsal view, the zygosphene (zs.) anterior margin is slightly lobed. The neural spine (n. s.) is longer than it
48 is high. The synapophysis (sy.) is well individualized with a diapophysis slightly bigger than the
49 parapophysis. The prezygapophyseal processes (pz. pr.) are conical, thick, blunt, laterally oriented and
50 their length correspond to half of the prezygapophyseal facet (prz. f.) length. Paracotylar foramina (p. f.)
51 are present on each side of the condyle. From a lateral view, the hemal keel (h. k.) is well marked.
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55 On the basis of these features, these vertebrae can be ascribed to a colubroid snake. In addition, the
56 prezygapophysis morphology, thicker and more laterally oriented than those of the other Cadet 2
57 colubroid vertebrae, allows us to advocate their attribution to the genus *Alsophis*. These vertebrae occur
58 in all the Cadet 2 layers.
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4 Colubroidea sp. 1 – 13 dorsal vertebrae.
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6 These vertebrae (Fig. 5 I) are similar to those previously described for cf. *Alsophis* sp., except that they
7 are smaller (maximal centrum length = 1.2 mm) and they bear longer, sharper and anteriorly oriented
8 prezygapophyseal processes (pz. pr.).
9

10
11 These vertebrae could possibly belong to a member of the genus *Liophis* (possibly *Erythrolamprus*
12 following Curcio et al., 2009), which is with *Alsophis* the only genus of colubroid snake ever observed on
13 Marie-Galante (Breuil, 2002), but the vertebral morphology of the latter is still undescribed and remains
14 unknown to us for the time being. These vertebrae occur in all the Cadet 2 layers.
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17 Colubroidea sp. 2 – 1 dorsal vertebra.
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20 This vertebra (Figs. 5 J-M) is similar to those previously described for cf. *Alsophis* but it presents some
21 significant differences. It bears a more marked neural arch median constriction than the other vertebrae
22 in dorsal view. The neural spine (n. s.) is also different; it is high and thin with anterior and posterior
23 borders slightly overhanging. The prezygapophyseal processes (pz. pr.) are shorter and thicker and the
24 prezygapophysis articular facets (prz. f.) have a more elongated shape.
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27 For the time being, we cannot suggest a specific attribution for this vertebra. It could be from an
28 unknown taxon from the island fauna. This single vertebra was recovered in the Locus 2 Pleistocene
29 layer.
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32 33 34 35 **Discussion** 36

37 We identified at least ten taxa in the different sampled layers of Cadet 2, all of which occur in the
38 Pleistocene layers, which are currently the oldest known Marie-Galante fossil levels. Consequently, our
39 study provides the first information on Marie-Galante Pleistocene fauna prior to 14,000 B.C. (Stouvenot
40 et al., 2014).
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43 Three taxa are only present in the Pleistocene layers at Cadet 2: *Boa* sp., Colubroidea sp. 2 and cf.
44 *Sphaerodactylus* sp. *Boa* sp. was previously reported at Cadet 3 (Stouvenot et al., 2014), where, like at
45 Cadet 2, this taxon only occurs in Pleistocene levels. Colubroidea sp. 2 had not been identified up until
46 now but this attribution will require further investigation. *Sphaerodactylus* is a very small
47 sphaerodactylid gecko still occurring on Marie-Galante (Breuil, 2002; Powell and Henderson, 2012). This
48 is the first fossil record of this taxon on the island and it shows that it was already present there during
49 the late Pleistocene. This is not surprising given the existence of a Marie-Galante endemic sub-species
50 (*Sphaerodactylus fantasticus adrinotus*) (see Breuil, 2002), which was the first evidence of its local
51 evolution on the island.
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56 The other identified taxa have been previously observed alive on the island and occur in all the Cadet 2
57 layers. This is the case for the *Eleutherodactylus* frogs, currently represented on the island by two
58 species: *E. marticensis* and *E. johnstonei* (Breuil, 2002; Powell and Henderson, 2012). The Marie-Galante
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4 skink (cf. *Capitellum mariagalantae*) was observed on the island for the last time in 1830 and is since
5 considered to be extinct (Hedges and Conn, 2012). This taxon is also present in the Cadet 3 site
6 (Stouvenot *et al.*, 2014). Ameivas were reported for the last time in the 17th century (see Breuil, 2002).
7 This taxon is also present in several other Marie-Galante sites (Grouard, 2001; Grouard, 2003; Stouvenot
8 *et al.*, 2014). Anoles (*Anolis cf. ferreus*) are still widely present on the island (Breuil, 2002) and fossil
9 anole remains have already been mentioned at other sites (Grouard, 2001; Grouard, 2003; Stouvenot
10 *et al.*, 2014). As for the snakes, *Antillotyphlops* is considered to have become extinct very recently on
11 Marie-Galante (Breuil, 2002), *Alsophis* disappeared from Marie-Galante during the 20th century (Breuil,
12 2002) and *Liophis* (Colubroidea sp. 1?) even earlier at the end of the 19th century (Henderson, 1992).
13 Bones from these three snakes were also reported at Cadet 3 (Stouvenot *et al.*, 2014).
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18 Evolution of the species composition (Fig. 6)

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21 Our data shed light on the herpetological biodiversity stability during the Pleistocene and Holocene
22 periods. Accordingly, only two taxa (*Boa* sp. and Colubroidea sp. 2) seem to have disappeared between
23 Pleistocene and Holocene periods. At the present time, this fact is difficult to explain due to the lack of
24 Pleistocene environmental data for the island. The case of the boa, still represented in the Lesser Antilles
25 on Dominica (*Boa nebulosa*) and Saint Lucia (*Boa orophias*) by endemic taxa, is very interesting but the
26 study of larger series is indispensable to enhance our knowledge of the taxonomic status, biological
27 features and extinction causes of this snake.
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31 This apparent stability no longer subsists for the extant island fauna. Among the seven taxa that appear
32 to be present since the Late Pleistocene in Cadet 2, only three of them still occur on the island today
33 (*Eleutherodactylus* sp., cf. *Sphaerodactylus* sp. and *Anolis cf. ferreus*). Ameivas, skinks and all the snakes
34 are now extinct. This fact, combined with the occurrence of these taxa in the most recent Cadet 2 layers,
35 in the late Holocene Cadet 3 layers (Stouvenot *et al.*, 2014) and historical mentions of these taxa (see
36 Breuil, 2002) shows that these extinctions occurred during the last few centuries, after European
37 colonization. Many explanations can be advanced to account for these extinctions, which are widespread
38 in all anthropized insular systems. In the Lesser Antilles, they are generally explained by the introduction
39 of new predators such as the mongoose (*Herpestes javanicus*), which was introduced by man in order to
40 eradicate rats and venomous snakes (Henderson, 1992; Henderson, 2004; Lorvelec *et al.*, 2004), but this
41 probably just represents one factor among others, such as habitat destruction or the introduction of new
42 competitors.
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48 However, all taxa were not impacted in the same way and the first data concerning fossil anole size
49 shows that the size of this taxon has remained the same from the Late Pleistocene until the present, for
50 a period of more than 30,000 years. Our data do not seem to comply with the taxon cycle theory and the
51 supposed classical existence of a second anole species on the island (Roughgarden, 1995). This also
52 shows that *Anolis ferreus*, still common on the island today, seems to display greater resilience to human
53 impact than most of the other currently extinct squamate taxa. Unlike other local squamates, this anole
54 is mostly arboreal and this trait may have protected it from terrestrial allochthonous predators.
55 However, this explanation alone is not necessarily the only cause for the persistence of this taxon and
56 the observed patterns of extinction may also be explained with multifactorial models.
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4 Conversely, some frog and squamate taxa that do not occur in Cadet 2 are now present on the island.
5 Predictably, some of them are commonly recognized as recently introduced taxa: *Scinax cf. x-signatus*,
6 *Hemidactylus mabouia*, and *Gymnophthalmus underwoodi*, but some of the others were previously
7 thought to be natives or of uncertain status. The Turnip-tailed gecko (*Thecadactylus rapicauda*), for
8 instance, is absent from Cadet 2 and only occurs in a Cadet 3 layer dated to around 1,000 AD (Stouvenot
9 *et al.*, 2014). The absence of earlier fossil remains of this species could be further evidence of its recent
10 arrival on the island. Another interesting case is the absence of iguanas in the fossiliferous localities
11 while this taxon is present in pre-Columbian archaeological deposits (Grouard, 2001, 2003, 2007, 2010;
12 Bochaton, com. pers.), a fact that could also be related to their recent arrival. The Curly-tailed lizard
13 (*Leiocephalus cf. cuneus*) is also absent from Cadet 2, but present in Cadet 3 in deposits possibly
14 contemporaneous with a pre-Columbian occupation layer and now extinct on the island. In the same
15 way as the iguana, the absence of this species in Cadet 2 is hard to explain and both taxa may possibly
16 have been introduced on the island by human populations. An overview of all the fossil and subfossil
17 herpetological data is still in progress in order to test these hypotheses and to clearly define the
18 colonization scenario for each taxon in Marie-Galante, and more generally in the Guadeloupe islands.
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25 **Conclusion**

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27 Only three out of the ten indigenous reptile and amphibian taxa occurring in the Pleistocene layers of
28 Cadet 2 on Marie-Galante are still extant on the island (*Anolis cf. ferreus*, *Sphaerodactylus fantasticus*
29 and *Eleutherodactylus* sp.), which points to an extinction rate of at least 70 %. Among those extinctions,
30 only two (*Boa* sp. and Colubroidae sp. 2) are probably anterior to the human occupation of the island
31 because they only occur only in Pleistocene layers. But most of the herpetofauna, which remained stable
32 for more than 30,000 years, was eliminated and replaced during the past two or three centuries. The
33 Marie-Galante herpetofauna seems to be a demonstration of what is generally called the present sixth
34 mass extinction crisis (Barnosky *et al.*, 2011). This massive extinction is directly linked to human impact
35 on the biosphere. Our approach also confirms the importance of integrating fossil and subfossil data to
36 enhance our comprehension of the dynamics of herpetological communities after anthropization.
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44
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Figure 1: Site location and stratigraphy of the first locus with radiocarbon dates.

Figure 1: Localisation du site et stratigraphie du premier locus avec datations radiocarbones.

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4 **Figure 2: *Eleutherodactylus* sp. - A and B: Maxillary, labial and lingual views; C: Vomer, dorsal view. *Anolis* cf. *ferreus* - D:**
5 **Maxillary, lingual view; E: Frontal, ventral view; F: Dentary, lingual view.**
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7 **Figure 2: *Eleutherodactylus* sp. - A et B: Maxillaire, vue labiale et linguale ; C: Vomer, vue dorsale. *Anolis* cf. *ferreus* - D:**
8 **Maxillaire, vue linguale ; E: Frontal, vue ventrale ; F: Dentaire, vue linguale.**
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12 **Figure 3: A: Distribution of the Snout-Ventral length (SVL) estimated from the dentaries dental length of *Anolis* cf. *ferreus* in**
13 **the Holocene and Pleistocene Cadet 2 layers. B: Histogram containing all the estimated SVL of the fossils and Gaussian**
14 **distributions resulting of a Gaussian mixture analysis.**
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16 **Figure 3: A: Distribution des longueurs museau-cloaque (SVL) estimée à partir des longueurs des rangées dentaires d'*Anolis* cf.**
17 ***ferreus* dans les niveaux d'âge Holocène et Pléistocène de Cadet 2. B: Histogramme de toutes les tailles estimées sur les**
18 **fossiles et distributions gaussiennes résultants d'une analyse de mélanges gaussiens.**
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22 **Figure 4: Cf. *Capitellum mariagalantae* - A and B: Frontal, dorsal and ventral views; C and D: Dentary, labial and lingual views;**
23 **E: Articular-prearticular, dorsal view. *Ameiva* sp - F: Maxillary, lingual view; G and H: Frontal, ventral and dorsal views; I:**
24 **Dentary, lingual view.**
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26 **Figure 4: Cf. *Capitellum mariagalantae* - A et B: Frontal, vues dorsale et ventrale ; C et D: Dentaire, vues labiale et linguale ; E:**
27 **Articulaire-préarticulaire, vue dorsale. *Ameiva* sp - F: Maxillaire, vue linguale ; G et H: Frontal, vues ventrale et dorsale ; I:**
28 **Dentaire, vue linguale.**
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32 **Figure 5: Cf. *Antillotyphlops* - A-B: dorsal vertebra, dorsal and ventral views; *Boa* sp - C-E: dorsal vertebra, dorsal, lateral and**
33 **anterior views; Cf. *Alsophis* sp. - F-H: dorsal vertebra, dorsal lateral and anterior views; Colubroidae sp. 1 - I: dorsal vertebra,**
34 **dorsal view; Colubroidae sp. 2 - J-M: dorsal vertebra, dorsal, ventral, lateral and anterior views.**
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36 **Figure 5: Cf. *Antillotyphlops* - A et B: vertèbre dorsale, vues dorsale et ventrale ; *Boa* sp. - C-E: vertèbre dorsale, vues dorsale,**
37 **latérale et antérieure ; Cf. *Alsophis* sp. - F-H: vertèbre dorsale, vues dorsale, latérale et antérieure ; Colubroidae sp. 1 - I:**
38 **vertèbre dorsale, vue dorsale ; Colubroidae sp. 2 - J-M: vertèbre dorsale, vues dorsale, ventrale, latérale et antérieure.**
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42 **Figure 6: Table containing the distribution of the taxa in the Cadet 2 and 3 (Sierpe, 2011; Stouvenot et al., 2014) layers along**
43 **with their historical mentions (see Breuil, 2002), present occurrence (Powell and Henderson, 2012) and minimal period of**
44 **occurrence on Marie-Galante (in grey).**
45

46 **Figure 6: Tableau de distribution des taxons dans les niveaux de Cadet 2 et 3 (Sierpe, 2011; Stouvenot et al., 2014) avec leurs**
47 **mentions historiques (voir Breuil, 2002), leur présence actuelle (Powell et Henderson, 2012) et leur période minimale de**
48 **présence à Marie-Galante (en gris).**
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53 **Appendix 1 : Compative specimens used**
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55 *Ameiva* cf. *bifrontata* (MNHN-UMR 7209-343); *Ameiva chrysoleama* (MNHN-ZA-AC 1944-74); *Ameiva plei*
56 (MNHN-RA 1991.4275; MNHN- UMR 7209-405); *Ameiva surinamensis* (MNHN-RA 1991.4034); *Ameiva*
57 *undulata* (MNHN-RA 1991.4276); *Anolis desiradei* (UMR-5199 201111-A; UMR-5199 221111-A; UMR-
58 5199 231111-A; UMR-5199 250311-A; UMR-5199 251111-A); *Anolis ferreus* (UMR-5199 071111-A; UMR-
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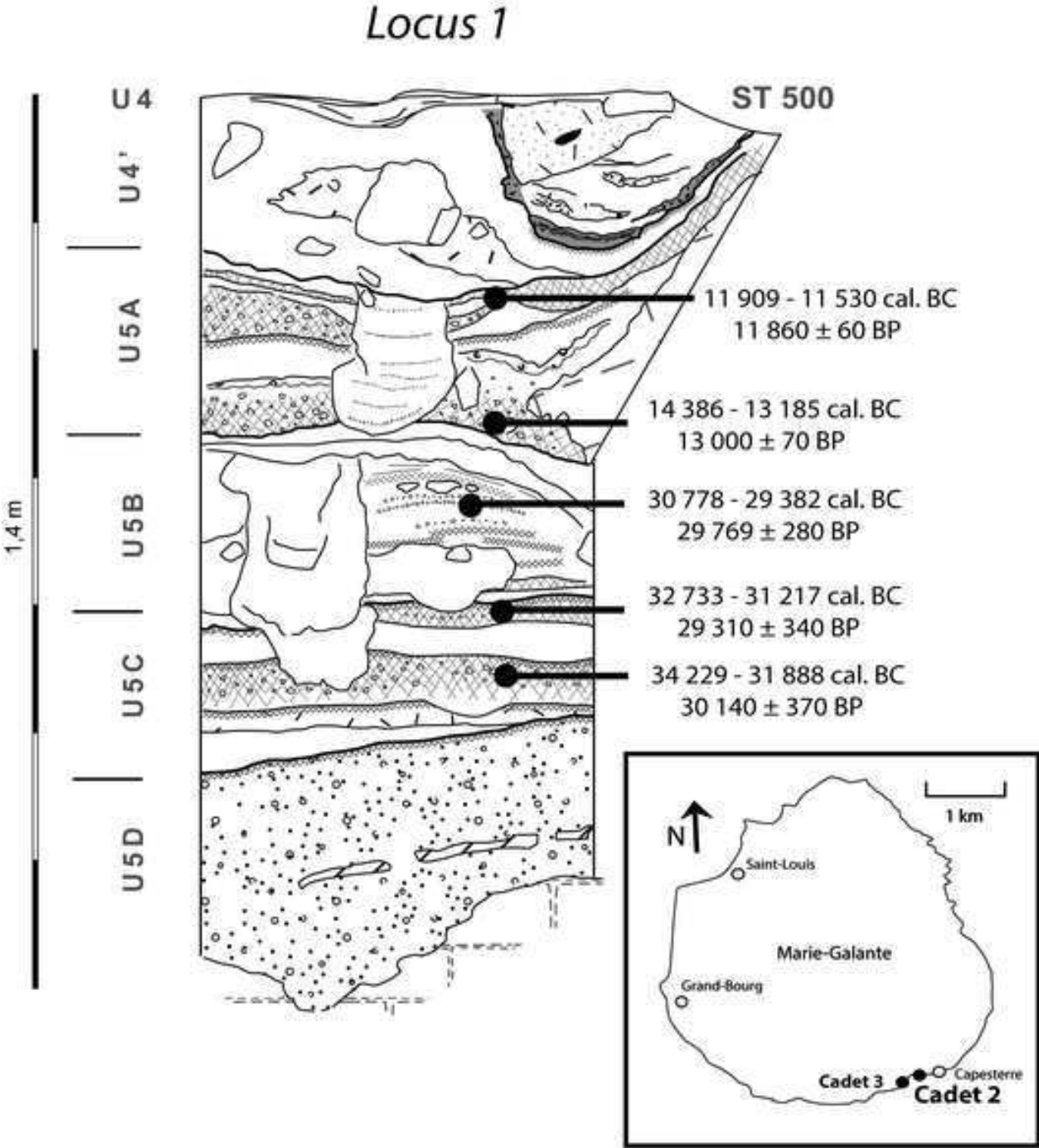
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5199 161111-A; UMR-5199 161112-B; UMR-5199 181112-A; MNHN-UMR 7209-655; MNHN-UMR 7209-656; MNHN-UMR 7209-674; MNHN-UMR 7209-675; MNHN-UMR 7209-676; MNHN-UMR 7209-677; MNHN-UMR 7209-678; MNHN-UMR 7209-679; MNHN-UMR 7209-680; MNHN-UMR 7209-681; MNHN-UMR 7209-682; MNHN-UMR 7209-683; MNHN-UMR 7209-684; MNHN-UMR 7209-692); *Anolis marmoratus* (MNHN-UMR 7209-41; MNHN-UMR 7209-238; MNHN-UMR 7209-239; MNHN-UMR 7209-240; MNHN-UMR 7209-242; MNHN-UMR 7209-243; MNHN-UMR 7209-245; MNHN-UMR 7209-246; MNHN-UMR 7209-247; MNHN-UMR 7209-248); *Anolis pogus* (MNHN-UMR 7209-687; MNHN-UMR 7209-688; MNHN-UMR 7209-689); *Anolis roquei* (MNHN-UMR 7209-372; MNHN-UMR 7209-404a; MNHN-UMR 7209-404b; MNHN-UMR 7209-686); *Hemidactylus mabouia* (MNHN-UMR 7209-409; MNHN-UMR 7209-697); *Leiocephalus carinatus* (MNHN-UMR 7209-685); *Mabuya multifasciata* (MNHN-ZA-AC 1942-52); *Sphaerodactylus macrolepsis* (MNHN-UMR 7209-696; MNHN-UMR 7209-697); *Thecadactylus oskrobapreiorum* (MNHN-UMR 7209-693) ; *Thecadactylus rapicauda* (UMR-5199 160312-A).

Alsophis antillensis (MNHN-UMR 7209-17); *Alsophis rijgersmaei* (MNHN-UMR 7209-406); *Boa constrictor constrictor* (MNHN-ZA-AC 1876-250; MNHN-UMR 7209-335; MNHN-UMR 7209-672).

Eleutherodactylus johnstonei (MNHN-UMR 7209-53; MNHN-UMR 7209-403a; MNHN-UMR 7209-403b; MNHN-UMR 7209-403c; MNHN-UMR 7209-403d; MNHN-UMR 7209-403e; MNHN-UMR 7209-403f; MNHN-UMR 7209-403g; MNHN-UMR 7209-403h; MNHN-UMR 7209-407); *Eleutherodactylus martinicensis* (MNHN-UMR 7209-410; MNHN-UMR 7209-671).

Figure 1 - Stratigraphy
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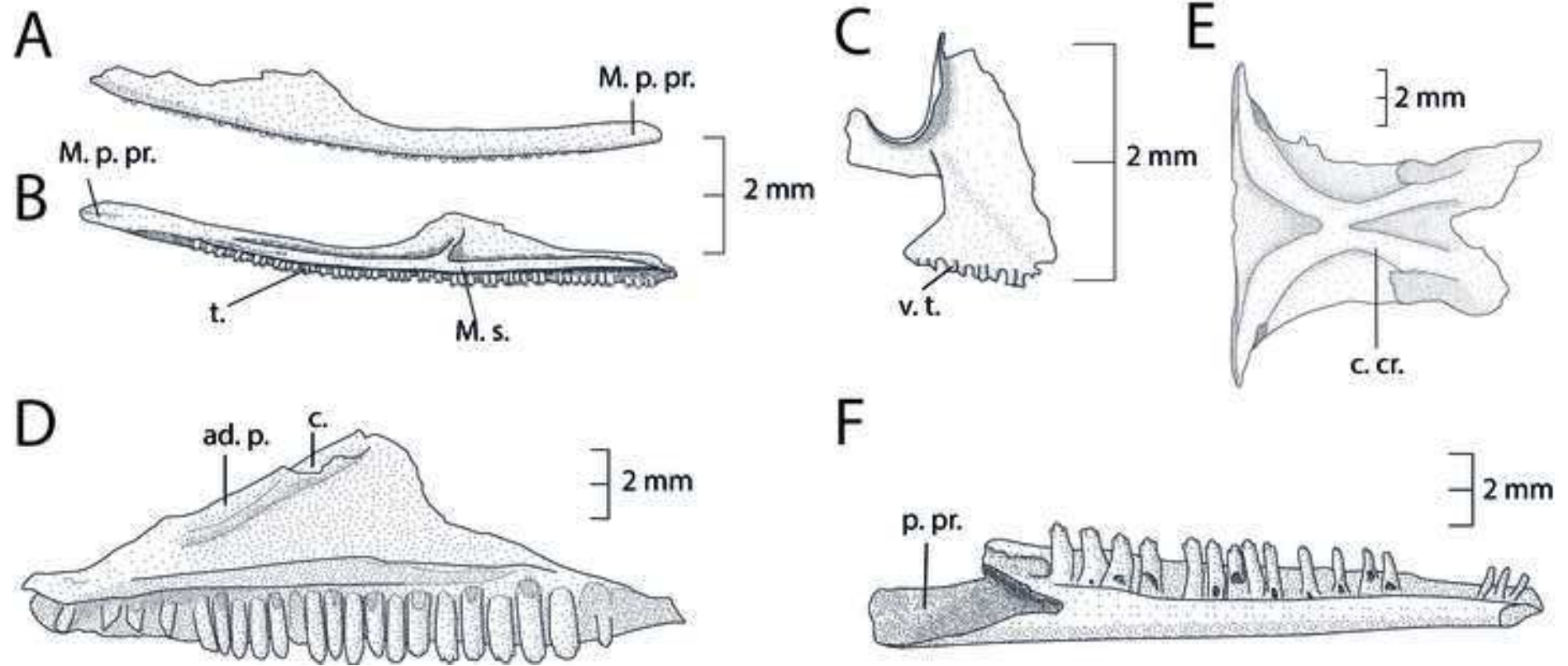
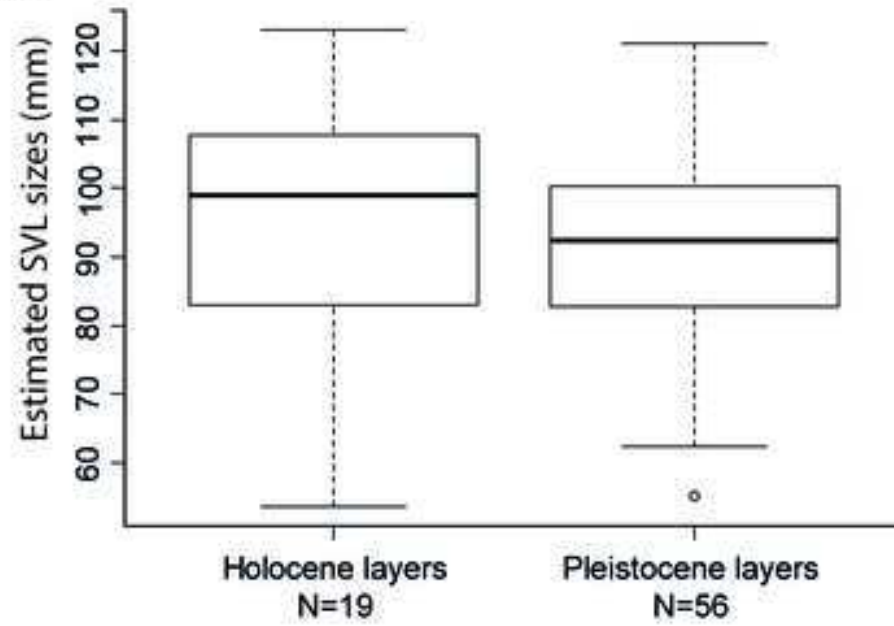


Figure 3 anoles sizes

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B

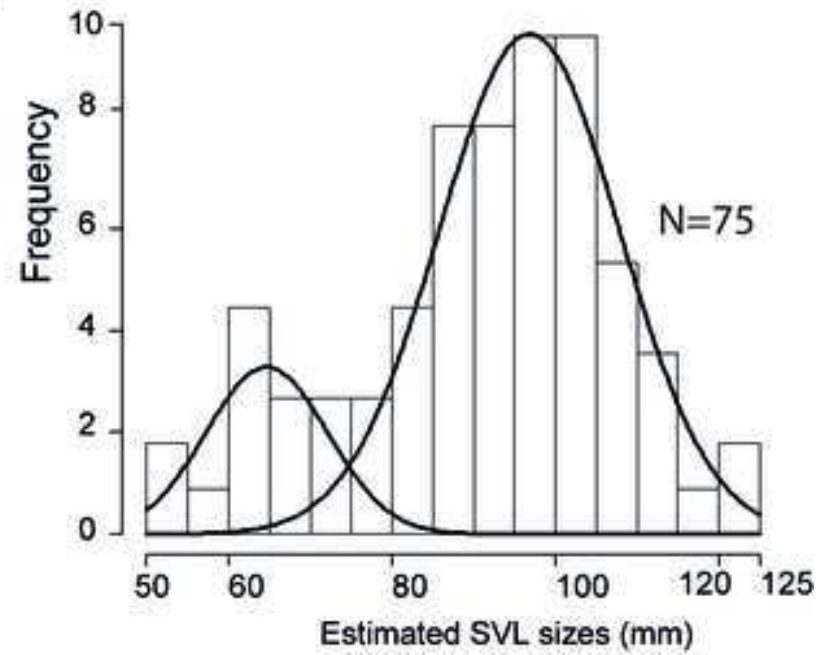


Figure 4 drawing
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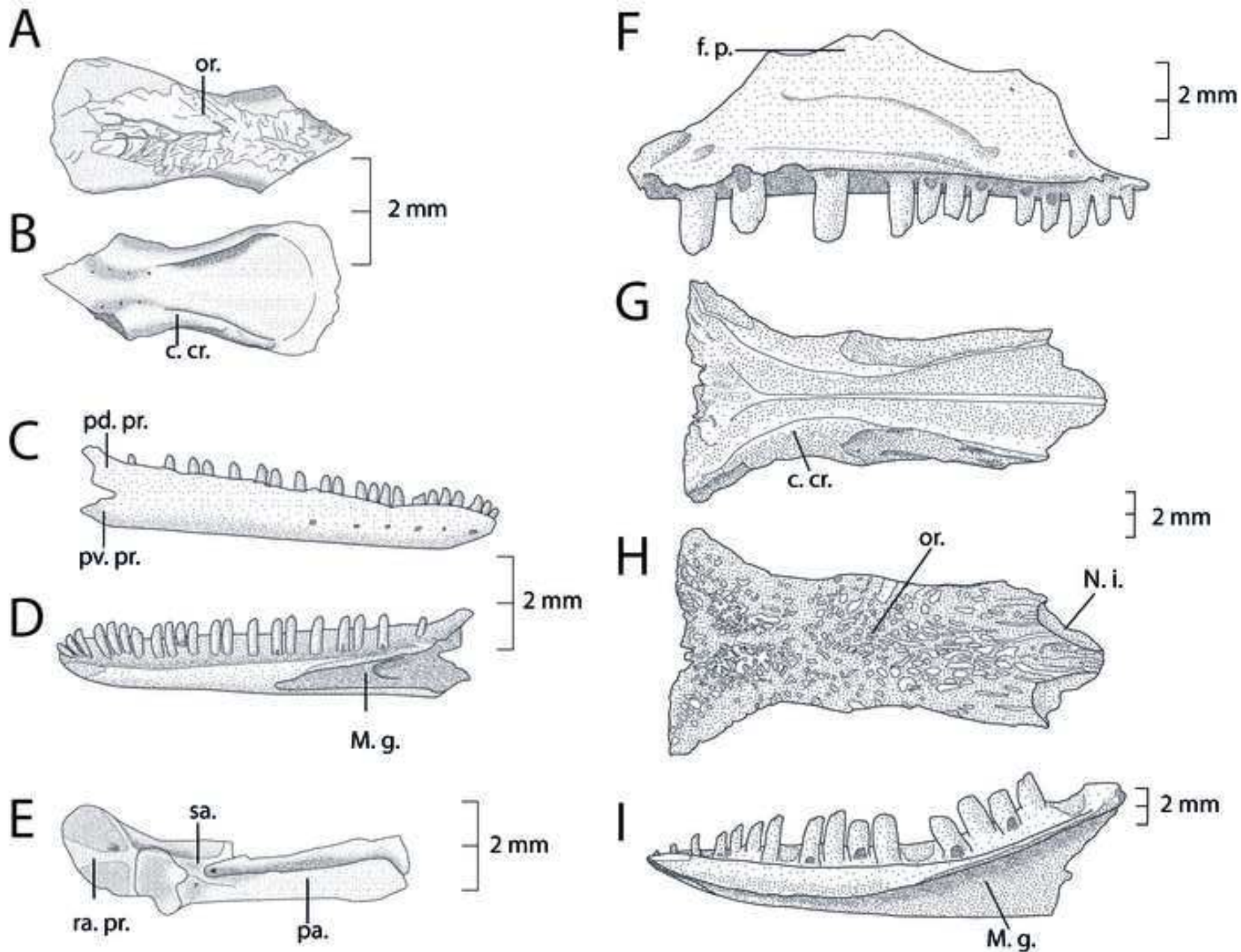


Figure 5 drawing

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