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QUATERNARY OCCURRENCE OF THE RARE LAND SNAIL *AMPHIBULIMA PATULA* (BRUGUIÈRE, 1789) IN GUADELOUPE (MOLLUSCA; AMPHIBULIMIDAE): ECOLOGICAL AND PALAEOENVIRONMENTAL IMPLICATIONS



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ABSTRACT

Amphibulima patula (Bruguière, 1789) is a rare native terrestrial mollusc from Guadeloupe. The past distribution of this species, assessed by shells collected from archaeological sites, natural deposits or surface surveys, shows it previously had a wider distribution that extended across all the limestone islands of the Guadeloupe archipelago. Stratigraphical contexts and radiocarbon data suggest that the presence or abundance of *A. patula* is related to periods of wetter environmental or climatic conditions, indicating that environmental factors influenced past variations in the distribution of this species. Its limitation to rare ecological refuges in periods of dry climatic conditions, combined with human-induced landscape modifications, have led to significant reductions in the numbers of individuals of this species that is today threatened with extinction in the Guadeloupe Islands.

Keywords : *Amphibulima patula*, Terrestrial malacofauna, West Indies, climate change, Human impact, faunal extinction

RÉSUMÉ

DISTRIBUTION QUATERNAIRE D'UN ESCARGOT RARE EN GUADELOUPE, *AMPHIBULIMA PATULA* (BRUGUIÈRE, 1789) (MOLLUSCA; AMPHIBULIMIDAE): IMPLICATIONS PALÉOENVIRONNEMENTALES ET ÉCOLOGIQUES

L'Ambrette capuchon, *Amphibulima patula* (Bruguière, 1789), est un escargot indigène rare en Guadeloupe, connu en Grande Terre et, historiquement, à Marie-Galante. Les coquilles collectées en site archéologique, en site géologique ou lors de prospections malacologiques, témoignent d'une distribution de ce taxon plus étendue par le passé qu'à l'actuel, couvrant l'ensemble des îles calcaires de l'archipel guadeloupéen. Les données géologiques, stratigraphiques et chronologiques montrent que la présence et l'abondance d'*A. patula* se corrèlent à l'optimum humide de l'Holocène, ou à un contexte de plaine littorale humide pour les coquilles recueillies dans les dépôts du dernier interglaciaire, suggérant par là-même que les facteurs environnementaux ont contrôlé les variations passées de l'aire de distribution de cette espèce. Une distribution limitée à de rares refuges écologiques en période sèche, combinée à une dégradation humaine des milieux, a conduit à une réduction significative de l'abondance de cet escargot aujourd'hui proche de la disparition en Guadeloupe.

Mots-clés : *Amphibulima patula*, malacofaune terrestre, Antilles, changements climatiques, modification humaine du milieu, disparition d'espèces animale

1 - INTRODUCTION

The islands of Guadeloupe are small oceanic islands that home to an original terrestrial mollusc fauna comprising twelve species endemic to the islands themselves and thirteen species endemic to the Lesser Antilles. With a total of seventy-three taxa characterized to species or subspecies, the Guadeloupean terrestrial molluscs form a rich, highly varied faunal community (Charles, 2016), and represent a potential source of powerful palaeoenvironmental proxies. However, Quaternary land snails are

rarely considered in palaeoenvironmental reconstructions for the West Indies with the notable exception of Jamaica. On this island, terrestrial mollusc shells recovered from a significant number of Pleistocene and Holocene deposits (Goodfriend & Mitterer, 1988, 1993; Paul & Donovan, 2005; Donovan & Paul, 2010, 2013) have provided a uniquely detailed record of Quaternary faunal changes in the New World tropics (Goodfriend, 1993).

In the Lesser Antilles, the use of terrestrial molluscs in palaeoenvironmental reconstructions is currently limited to a single study of carbon and oxygen stable isotopes

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measured from shells collected during archaeological excavations (Beets *et al.*, 2006). However, Yanes & Romanek (2013) have shown that on tropical islands this type of approach faces important issues connected to the uptake of dead carbon by snails or the strong influence of local conditions, both a source of important variability in isotopic content that precludes any precise depiction of past environmental conditions. Consequently, taxonomic composition of fossil land snails is a potentially better yet still underexplored proxy for palaeoenvironmental reconstructions.

One reason why land snails remain a neglected source of palaeoenvironmental information in the Caribbean is the still limited understanding of species distributions or abundances in relation to different environmental contexts (Goodfriend, 1992). Determining environmental conditions from a given species relies on accurately establishing the range of biomes or relevant physical (*e.g.* altitude) and climatic variables (*e.g.* annual rainfall, mean temperature) in which the species can be observed (*e.g.* Goodfriend, 1987). This procedure is relatively easy when a large set of occurrence data exists, but is unfeasible when only a small number of observations are available, as is the case with rare species. However, it is precisely because of their rarity that poorly documented or rare species are unlikely to contribute in any significant manner if at all to the fossil record. Thus, limited data concerning rare species would only be a limiting factor in instances involving previously abundant species, particularly when changes in species distribution can be linked to environmental changes therefore eliminating an important source of evidence for taxonomically-based palaeoenvironmental reconstruction.

A now rare but formerly common species from Guadeloupe is *Amphibulima patula* (Bruguière, 1789). Shells of this native terrestrial land snail are found on a significant number of archaeological or natural sites, sometimes in important quantities. This species, endemic to the Lesser Antilles, has been reported from the islands of Dominica, Guadeloupe, Marie-Galante, St. Kitts and Saba (Pilsbry, 1899). On Guadeloupe, however, this mollusc, the largest of the native terrestrial species, has disappeared during the nineteenth century from localities documented during the colonial period. Subsequently, apart from a single live snail observed some 15 years ago (obs. A. Bertrand), only empty shells have been documented. This illustrates that this species, still common on the neighbouring island of Dominica (Robinson *et al.*, 2009), is extremely rare on Guadeloupe.

Here we compare the historical and present distribution of *Amphibulima patula* to fossil shells recovered during archaeological excavations, buried in natural deposits or collected during surface surveys. These data are subsequently used to map changes in the distribution of this species over time. The age of the deposits and the geomorphological setting of the localities that have yielded specimens of *A. patula* are also considered to investigate potential correlations between variations in the snail occurrence and/or abundance and environmental

changes. Hence, a larger set of observations is used to overcome the scarcity of modern occurrence data and identify environmental conditions favouring the occurrence of *Amphibulima patula*. Finally, the results allow us to discuss whether the current rarity of this land snail species is a response to climatically-driven or human-induced landscape modifications.

2 - MATERIAL AND METHODS

The islands of Guadeloupe are situated at the junction between the Windward and Leeward Islands of the Lesser Antilles. The main island, Guadeloupe, is composed of two adjacent islands separated by a narrow stretch of water – the western volcanic island of Basse-Terre and eastern limestone island of Grande-Terre. The archipelago also includes a number of smaller limestone islands (Marie-Galante, Désirade, Petite-Terre) and volcanic islets (Les Saintes, fig. 1).

With a maximum elevation of 1467 m, Basse-Terre is characterised by an altitudinal gradient in rainfall determining a vertical zonation in vegetation, where dry forest on the coast gives way to moist semi-evergreen forest at middle altitudes and then rain forest in higher areas. The maximum elevation of the other islands varies between 200 and 300 metres, resulting in a secondary dry forest that grades into an intermediate xeric-mesic forest only in the western part of the larger Islands of Grande-Terre and Marie-Galante (Lasserre, 1961).

Previous information concerning *Amphibulima patula* on Guadeloupe was collected from both published scientific literature and unpublished reports of the *Direction de l'Environnement, de l'Aménagement et du Logement* relating to the malacofauna of Guadeloupe (Bouchet & von Cosel, 1991; Bouchet & Pointier, 1998; Bertrand, 2001; Charles, 2015). Pre-Columbian and historical archaeological collections kept by the *Service Régional de l'Archéologie* at Moule were reviewed in order to identify the occurrence of *A. patula* shells in archaeological sites, as were publications and unpublished reports housed at the *Direction des Affaires Culturelles de Guadeloupe* on Basse-Terre. This information was supplemented by our own unpublished observations of old and fossil *A. patula* shells. All previously reported and newly documented occurrences of *A. patula* were plotted with a GPS. In the case of old shells (*i.e.* shells without periostracum collected from the ground), ecological conditions were recorded, while for fossil shells (*i.e.* shells recovered from archaeological or natural deposits), the geomorphological context, nature of sediment, and stratigraphical position were also noted.

All radiocarbon ages include laboratory references and are expressed in calibrated ages at 2 sigma (95.6 %) probability. The Marine13 calibration curve was used for dates obtained from marine shells and both Marine13 and Intcal13 curves for human bones (Reimer *et al.*, 2013) using a linear interpolation of the bone collagen $\delta^{13}C$ values (Petchey & Grenn, 2005).

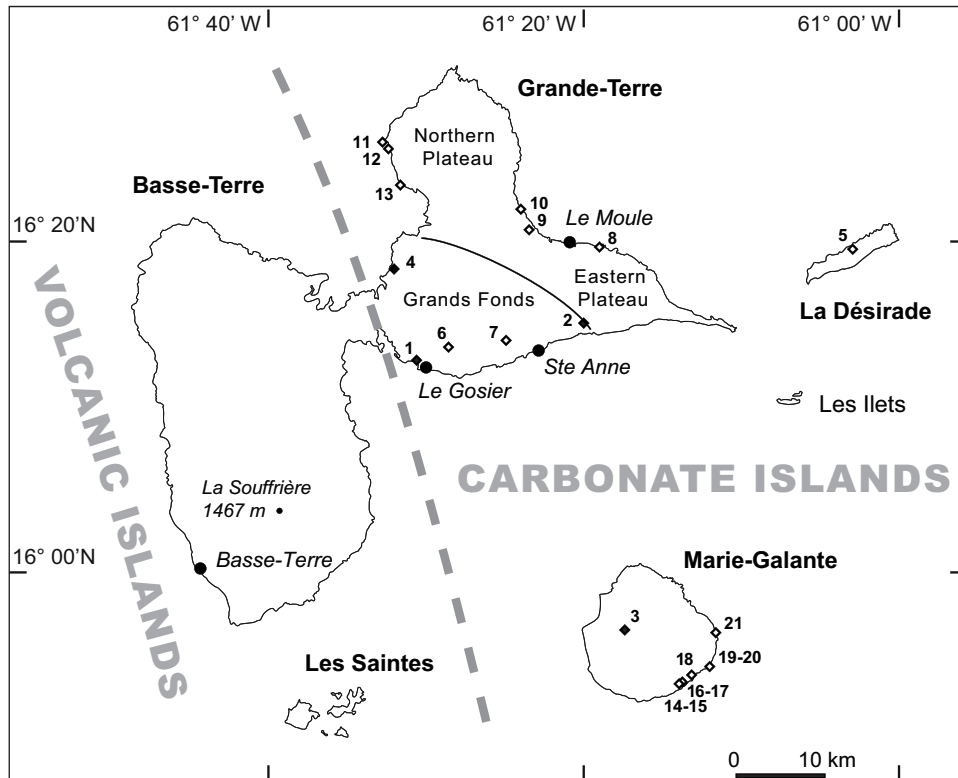


Fig. 1: Distribution map of *Amphibulima patula* localities on Guadeloupe.

Historical and current stations are indicated by black diamond and localities with old or fossil shells by white diamond. The numbered localities refer to tables 1 and 2.

Fig. 1 : Carte de distribution des stations d'*Ambrette capuchon*, *Amphibulima patula*, dans l'archipel de Guadeloupe. Les stations historiques et actuelles sont figurées par des losanges noirs et les stations livrant des coquilles fossiles ou anciennes par des losanges blancs. La numérotation des stations est celle des tableaux 1 et 2.

3 - RESULTS

3.1 - HISTORICAL AND PRESENT LOCALITIES OF *AMPHIBULIMA PATULA* ON GUADELOUPE

Amphibulima patula was first described from Guadeloupe by Bruguière (1789: 305-306) towards the end of the eighteenth century, although no detailed locality information was provided. The author held that a Mr. Badier, a naturalist, who lived on Guadeloupe in the 1780-1790s and was referred to by Bruguière as an "excellent observer", was unable to tell if this species was terrestrial or fluvial, suggesting that even at this early date *A. patula* was not commonly observed on the Island.

The species was described a second time by Lamarck (1805), based on a purchased specimen without location, making impossible to know whether this specimen was actually found on Guadeloupe. The only specimens

known from the island in the early nineteenth century are those used by Férussac for his "*Histoire naturelle des mollusques*" (Férussac, 1821). As some are still preserved in alcohol (Chevallier, 1965), they were collected as live specimens, presumably at the end of the eighteenth century or in the early nineteenth century. According to Mazé (1883), no living specimen was collected on Guadeloupe thereafter.

Paradoxically, historical localities were recorded by Beau (1857), Schramm (1873), Mazé (1883), while living *Amphibulima patula* was no longer found. Indeed, these localities were determined based on fresh shells (tab. 1). These are the Bois Boivin on St. Anne, where Schramm found two shells in the first half of the nineteenth century, and the shore of Fort Union on Gosier, where Beau collected two specimens retaining their periostracum (Schramm, 1873; fig. 1). The first malacological inventory for the Guadeloupe Islands was

N	Locality		Location (WGS 84 system)		References
	Name	Island	longitude	latitude	
1	Fort-Union Bay	Grande-Terre	-61.5090	16.2152	Schramm 1873, Mazé 1883
2	Boivin Forest	Grande-Terre	-61.3419	16.2563	Schramm 1873, Mazé 1883
3	Ravine Potens	Marie-Galante	-61.2964	15.9358	Mazé 1876
4	Layon Lambis	Grande-Terre	-61.5352	16.3059	This study (obs. A. Bertrand 2001)

Tab. 1: Historical and current localities of *Amphibulima patula* on Guadeloupe. Coordinates are expressed in decimal degrees.

Tab. 1 : Stations actuelles et historiques d'*Amphibulima patula* en Guadeloupe. Les coordonnées géographiques sont exprimées en degrés décimaux.

published by Petit de la Saussaye, based on shells sent to him by Beau (Petit de la Saussaye, 1851, 1853, 1856). *A. patula* is absent from the original catalogue of 1851, but appears in the supplementary list of 1853 including shells newly collected by Beau. This provides a reliable indication of the Beau's specimens being collected in the early 1850s. After this date, reports contain records only of fossil specimens (Beau, 1857; Schramm, 1873; Mazé, 1883), notably in association with *Bulimulus guadalupensis* (Bruguière, 1789) and *Pleurodonte lychnuchus* (Müller, 1774) in deposits at the base of the Moule cliffs (Duchassaing, 1847; Schramm, 1873; Mazé, 1883).

Living snails were reported by Mazé on the neighbouring Island of Marie-Galante at Les Sources in the latter half of the nineteenth century (Mazé, 1876, 1883 and fig. 1) whereas only old shells were collected from the same location in 2000 by Verhaegue & Bertrand (Verhaegue Collection, Bertrand 2001) and in 2015 by Charles. Les Sources is currently covered by secondary forest, where the abundance of West Indian bay tree (*Pimenta racemosa*) indicates the area to have been cultivated during the historical period.

Lastly, a living *Amphibulima patula* was found in March 2001 at the edge of a freshwater swamp forest (*Pterocarpus officinalis*) bordering the mangrove on the west coast of Grande-Terre (tab. 1). Like Les Sources, this location provides the wet, shaded habitat associated with *A. patula* (Mazé, 1877).

3.2 - PAST DISTRIBUTION OF *AMPHIBULIMA PATULA* IN GUADELOUPE

Old or fossil shells of *Amphibulima patula* were collected in recent years on Grande-Terre, Marie-Galante, and La Désirade (fig. 1), which provides the first record of this species having once occurred on the latter island. Sixteen additional sites were identified in addition to the previously documented occurrence of *A. patula* at Moule (tab. 2). The age of the specimens can be relatively reliably dated according to the stratigraphical and/or geological context in which shells were found.

3.2.1 - Slope deposits

Fossil *Amphibulima patula* shells in natural contexts are most commonly found in slope deposits abutting the face of the last interglacial sea-cliff. This deposit is a reddish, cemented silty-carbonated sand, which can be rich in limestone rubble and occasionally contain abundant complete or fragmented shells. *A. patula* is never common in this deposit, which is characterised primarily by the presence of land snails of the families Bulimulidae and Pleurodontidae, the size of the Pleurodontidae suggesting *P. lychnuchus*, as at, for example, Anse à l'Ecu.

This species association and the geomorphological setting are comparable to the Moule locality in which fossil specimens were collected in the nineteenth century (Duchassaing, 1847). This slope deposit, which outcrops along the eastern coast of Grande-Terre as well as the south-eastern coast of Marie-Galante, has been assigned

to the Upper Pleistocene by Garrabé *et al.* (1988). *Amphibulima patula* is, however, not present in all outcrops; for example, the site of *La Pointe des Châteaux* on the easternmost point of Grande-Terre contains numerous *Pleurodonte lychnuchus*, large Bulimulidae and some *Diplopoma* sp. (Bertrand, 2001), but no *A. patula*.

The shell found in the course of archaeological excavations at the Stade J. Bade on Marie-Galante documents a slightly different geomorphological configuration. The slope deposit containing it overlies a lagoonal clay formed during a highstand of a substage of MIS 5 and is buried several metres below the modern barrier beach (Bertrand, 2012), indicating that it post-dates the last Interglacial and pre-dates modern landscape formation, which is in agreement with an Upper Pleistocene age.

Unlike the sites mentioned above, the site of Barbès in the Grands Fonds region of southwestern Grande-Terre lies in an area of karstic hills. A single fossil shell of *Amphibulima patula* was found in association with Bulimulidae and *Pleurodonte* sp. in a section of a road cut at the top of a limestone hill. This outcrop of unknown age comprises 0.4 m of colluvial deposits accumulated in depressions in the substrate, with shells included in the lower horizon of carbonate accumulation.

3.2.2 - Archaeological and palaeontological sites

Although both archaeological and palaeontological sites provide reliable chronological contexts, determining the exact age of *Amphibulima patula* shells is sometimes problematic, primarily due to difficulties in discerning whether shells are in a primary position.

The most recent site is the *grotte Blanchard 2* on Marie-Galante, which opens onto a fossil cliff ten metres above the coastal plain. A test pit within the cave documented a half metre of colluvial deposits for which the vertebrate faunal association and radiocarbon bone dating point to a formation between the fifteenth century and the early twentieth century (Mallye *et al.*, 2018). *Amphibulima patula* shells were found throughout the deposit as well as a test-pit on the slope above the cave, suggesting that the shells were introduced to the site by colluviation. Moreover, the shells frequently exhibit notches similar to those produced by snail-feeding birds (fig. 2), which, when considered alongside the site's geological context, suggest that the shells derive from a natural accumulation on the overlying slope (Mallye *et al.*, 2018.).

Amphibulima patula shells were collected on the ground as well as in a layer beneath a pre-Columbian burial at the entrance to the nearby but slightly older *grotte Blanchard*. A radiocarbon date obtained on a human bone provided an age of 1313-1439 CE (Erl. 10155; Stouvenot, 2005), placing the burial only few centuries before the use of *Blanchard 2* as a nesting ground. However, as the site opens at the base of a cliff directly below *Blanchard 2*, it is likely that the shells derive from the same accumulation on the slope above both caves. As with *Blanchard 2*, the shells could be older than the layers containing them.

Voûte à Pin on La Désirade is a pre-Columbian burial cave that shares a similar chronology with the previous

N	Locality		Location (WGS 84 system) longitude latitude	Type of site	References	Observations
	Name	Island				
5	Voûte à Pin	Désirade	-61.0484 16.3237	Cave infilling	this study	3 shells in the material coming from archaeological excavations (exc. M. De Waal 1999)
6	Barbès	Grande-Terre	-61.4922 16.2282	Colluvium deposit	this study	1 shell associated with Bulimulidae and <i>Pleurodonte</i> sp. (find. C. Stouvenot 2014)
7	Trace du Prince	Grande-Terre	-61.4150 16.2389	Surface, in a dry forest	this study	1 bleached shell in the soil associated with <i>Pleurodonte lychnuchus</i> bleached as well (find and coll. L. Charles 2009)
8	Tufs des falaises du Moule	Grande-Terre	- - -	Pleistocene deposits	Mazé, 1883	Several shells collected in the mid-nineteenth century, associated with <i>P. lychnuchus</i> and <i>Bulimulus guadalupensis</i> . Hypothetically located at a place called Morel, on the basis of the indications given by Duchassaing (1847)
9	Abri Patate	Grande-Terre	-61.3892 16.3486	Rockshelter infilling	Stouvenot 2004, A. Bertrand 2005	6 shells at the base of the infilling (couche D), associated with Bulimulidae, <i>Pleurodonte josephinae</i> and <i>P. lychnuchus</i> (exc. C. Stouvenot 2004).
10	Anse à l'Ecu	Grande-Terre	-61.3991 16.3703	Pleistocene deposits	this study	1 shell associated with large shells of <i>Pleurodonte</i> cf. <i>lychnuchus</i> and Bulimulidae (find. A. Lenoble 2014, coll. L. Charles)
11	Pointe d'Antigues	Grande-Terre	-61.5411 16.4369	Surface, in a dry forest	this study	1 complete shell on the ground of a dry forest (find. and coll. R. Péniisson 2009)
12	Pointe des Mangles 2	Grande-Terre	-61.5368 16.4320	Archaeological layer buried in a sandy beach	Stouvenot 2007	2 shells in an archaeological layer with an age of 171 BCE-304 CE (test-pit 7B, Unit 2) (exc. C. Stouvenot 2005)
13	Anse du Gris-Grès	Grande-Terre	-61.5242 16.3939	Surface, on the shore	this study	1 incomplete old specimen, grey (Find. and coll. L. Charles 2009)
14	Abri de Cadet 3	Marie-Galante	-61.2350 15.8820	Rockshelter infilling	Stouvenot et al. 2013	788 shells, in the mid- and upper part of the infilling (layer D to I), ranging from the mid-Holocene up to the last millennium, associated with <i>P. josephinae</i> , <i>B. guadalupensis</i> and <i>Diplopoma crenulatum</i> (exc. C. Stouvenot 2004).
15	Grotte Cadet 2	Marie-Galante	-61.2349 15.8820	Cave infilling	this study	2 shells in the material coming from old excavation spoiled sediment (unit II) (exc. P. Courtaud 2005-2007)
16	Grotte Blanchard 2	Marie-Galante	-61.2340 15.8822	Cave infilling	Mallye et al. 2012	87 shells in the whole infilling of the cave and 4 others shells in the sediment covering the upper slope (exc. J.-B. Mallye 2011)
17	Grotte Blanchard	Marie-Galante	-61.2339 15.8823	Rockshelter infilling	this study	2 shells on the ground (Find. A. Lenoble 2014) and two dozen in the infilling at the entrance of the cave (exc. C. Stouvenot 2005).
18	Stade J. Bade	Marie-Galante	-61.8895 15.2234	Pleistocene deposits	this study	1 shell collected in fossil slope deposit buried below modern barrier beach (exc. N. Serrand 2012).
19	Morne Rita	Marie-Galante	-61.2033 15.9026	Pleistocene deposits	this study	3 shells associated with few Bulimulidae and <i>Pleurodonte</i> sp. (find. C. Stouvenot 2013)
20	Grotte du Morne Rita	Marie-Galante	-61.2034 15.9034	Cave infilling	Fouéré et al. 2013	79 shells (exc. P. Fouéré 2011-2013) in colluvial layers with radiocarbon ages ranging between 0 and 2 500 BCE.
21	Morne à Boeuifs	Marie-Galante	-61.1979 15.9372	Pleistocene deposits	this study	1 shell associated with Bulimulidae and <i>Pleurodonte</i> cf. <i>josephinae</i> (find. J.-B. Mallye and N. Serrand 2014)

Tab. 2: Localities with fossil and old shells of *Amphibulima patula* on Guadeloupe.

find.: finding, exc.: excavations, coll.: collection.

Tab. 2 : Stations des îles de Guadeloupe à coquilles fossiles ou anciennes d'*Amphibulima patula*. find.: récolte, exc.: fouille, coll.: collection.

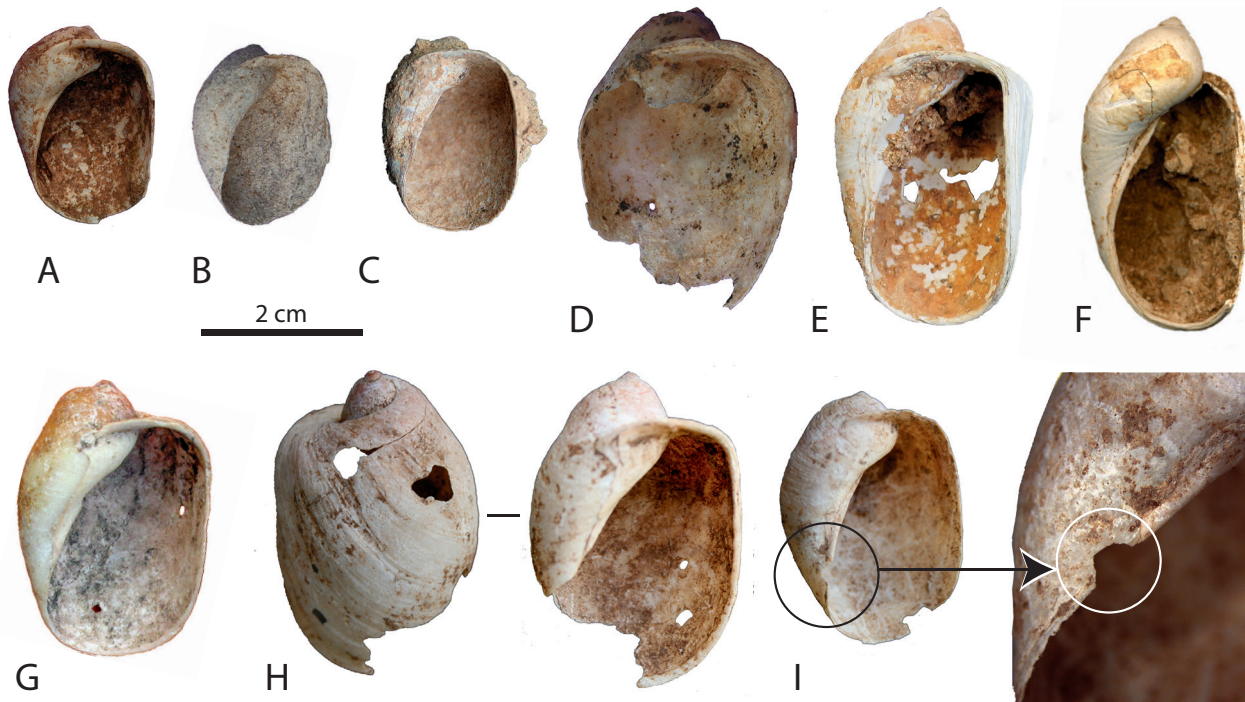


Fig. 2: Fossil shells of *Amphibulima patula* from the different Guadeloupe Islands localities.

A: Barbès, B: Pointe des Mangles 2, C: Voûte à Pin, D: Grotte du Morne-Rita, E: Morne à Bœufs, F: Abri Patate, G: Cadet 3, H, I: Blanchard 2, notched shell and detailed view of the notch (photo F: A. Bertrand, others: N. Serrand).

Fig. 2 : Coquilles fossiles d'*Ambrette capuchon*, *Amphibulima patula*, issues de différentes stations des îles de Guadeloupe. A: Barbès, B: Pointe des Mangles 2, C: Voûte à Pin, D: Grotte du Morne-Rita, E: Morne à Bœufs, F: Abri Patate, G: Cadet 3, H, I: Blanchard 2, coquille portant une encoche et détail de cette encoche (photo F: A. Bertrand, autres vues : N. Serrand).

site (Grouard *et al.*, 2014). Three *Amphibulima patula* shells were identified among the material recovered during M. De Waal's excavations. Unfortunately, these specimens were recovered from deposits disturbed by earlier excavations and therefore lack any reliable chronological information (De Waal, 2006).

The situation is similar at *Cadet 2*, a pre-Columbian cave dated to the same period, where two shells were identified among the material recovered from layer II composed of backfill from earlier, clandestine excavations (Courtaud *et al.*, 2005). These four sites therefore document *Amphibulima patula* shells in levels dated from the fourteenth to the early twentieth century. However, in all these cases, the reworked nature of the sediments or the possibility that the shells derive from remobilised accumulations do not exclude the snails being significantly older.

Examples of *Amphibulima patula* have, however, been reported from more reliable stratigraphical contexts. Two shells come from an archaeological level of Pointe des Mangles 2 located at a depth of between 30 and 40 cm in the present barrier beach. This well-characterised, ten centimetres thick archaeological level rich in marine shells and burnt stones is intercalated within nearly sterile sands (Stouvenot, 2007), effectively eliminating the likelihood of the shells being intrusive. Two radiocarbon dates on conch shell (*Lobatus gigas*), 85-390 CE (Erl - 9067) and 266 BCE- 72 CE (Erl 9068), place the archaeological occupation and, by extension, the *A. patula* specimens to the beginning of the Common Era.

Six other shells were identified in the preliminary malacological study of the *Abri Patate* material (Bertrand, 2005). These specimens, collected during a test pit within this rock-shelter, come from the deepest levels that sit directly on the bedrock approximately half a metre below the surface (Stouvenot, 2005). These lowermost levels contain *Amphibulima patula* and *Pleurodonte lychnuchus*, which are absent in the overlying levels dominated by *Pleurodonte josephinae* and *Bulimulus guadalupensis*, amongst others (Bertrand, 2005). A radiocarbon date obtained from a marine bivalve (*Codakia orbicularis*) found in the middle part of the test pit produced an age of 885-1155 CE (Erl-8232), indicating the land snail assemblage to have formed during or before the first millennium.

Seventy-nine shell fragments of *Amphibulima patula* were collected during archaeological excavations in the *grotte du Morne Rita* (Fouéré *et al.*, 2013). Apart from specimens included in the uppermost bioturbated level, *A. patula* remains are mainly associated with the lowermost colluvial unit, where several radiocarbon dates on charcoal and organic residues indicate an age ranging between 4 000 to 5 000 cal BP, and become rare in the uppermost colluvial horizon dated to between 2 000 and 4 000 cal BP (Fouéré *et al.*, 2015). This indicates both the presence of *A. patula* on the southern coast of Marie-Galante during the mid-Holocene and its subsequent reduction in abundance.

In addition to *Pleurodonte josephinae*, *Diplopoma crenulatum* and *Bulimulus* sp., 788 complete or frag-

mented *Amphibulima patula* shells were recovered from a test pit within the *Abri Cadet 3* on Marie-Galante. The stratigraphy of the rockshelter infilling consists of 5 layers. Radiocarbon dates indicate that the deposit documents a period ranging from the Late Pleistocene to the present (Stouvenot *et al.*, 2013). *A. patula* is abundant in the mid-Holocene level and well-represented up until the Amerindian level dated to between the first millennium BCE and the first millennium CE. The number of specimens decreases considerably in the overlying level corresponding to the last 1000 years. This is interpreted as being connected to the interruption of the natural accumulation process (snail-eating birds or surface run-off) responsible for introducing the shells to the site (Stouvenot *et al.*, 2013). In fact, shells of all snail species are rare in the uppermost level. Although the stratigraphy of *Cadet 3* demonstrates the considerable presence of *A. patula* on the south coast of Marie-Galante from the mid-Holocene to the first few centuries of the Common Era, it does not provide any relevant information concerning the eventual disappearance of this species.

3.2.3 - Old shell localities

No reliable age can be assigned to shells found on the ground insofar as these specimens may derive from older accumulations. This scenario is typically illustrated by shells found on the slope below the site of *Cadet 3*, where they undoubtedly derive from eroding deposits at the entrance of the shelter. Likewise, specimens collected on the west coast of the northern plateaus of Grande-Terre may originate from several thousands of years-older levels buried in the beach sand, as in the case of Pointe des Mangles 2. Despite their uncertain age, find spots where complete specimens were collected on the ground nevertheless reveal *A. patula* to have been more widely distributed in the past.

4 - DISCUSSION

Bouchet & Pointier (1998), following Mazé (1883), consider *Amphibulima patula* an extinct species on Guadeloupe, as neither a living individual nor any recent shells have been reported since the 1850s. However, the observation of one snail in 2001 demonstrates that, although rare and limited to a single location, this species still lives on Guadeloupe. Its extirpation from Marie-Galante is equally possible given the fact that no living specimen has been seen since those collected by Mazé in the late nineteenth century (Bouchet & Cosel, 1991). Similarly, the local extinction of *A. patula* on La Désirade is also more than likely, as no malacological surveys of the Guadeloupe Islands ever reported it living on the island (Mazé, 1883; Bouchet & Cosel, 1991; Bertrand, 2001; Charles, 2015). The identification of its former occurrence on La Désirade, as well as shells collected on Grande-Terre and the southern and eastern shores of Marie-Galante, show *A. patula* to have been more widely distributed in the past than previously thought, occurring

on all the limestone islands of the Guadeloupe archipelago.

The contrast between the historical and current distribution of *Amphibulima patula* on the one hand, and the distribution revealed by finds of fossil specimens, on the other, is all the more remarkable as the former correspond to wet localities meeting the ecological requirements of the species. Its amphibious nature (Mazé, 1876), inability to fully retract into its shell, nocturnal activity and habit of taking refuge under the broad leaves of banana trees (*Musa* sp.) or dumbcane (*Dieffenbachia seguine*) during the day led Mazé (1883) to consider this species to require moist, wooded areas such as the wet ravine bottoms where live snails were collected on Marie-Galante (Mazé, 1876). The swamp forest in which *A. patula* was seen living a decade ago fulfils these conditions. Similarly, the historical station of Fort Union Bay appears on eighteenth-century maps as a marshy plain (Ingénieurs du Roi, 1768), and *Bois Boivin* is a poorly drained section of one of the few river valleys on Grande-Terre. In contrast, fossil *A. patula* shells have been reported from dry forest environments, such as the shores of Grande-Terre and the southern areas of Marie-Galante, which do not fulfil the ecological requirements of the species, or even in arid environments such as the eastern shores of Marie-Galante (Rousteau *et al.*, 1994).

However, this difference is easily explainable when past environmental conditions are taken into account. For example, the current coastal plains of Grande-Terre and Marie-Galante were probably swamp environments during MIS 5 (~125 to 75 kyr). This is suggested by clay layers overlying the bedrock at several sites on Marie-Galante, which have been interpreted as marsh or lagoon sediments formed following the emergence of the previously submerged plain as a consequence of lowered sea-levels at the onset of the last glaciation (Bertran, 2012; Lenoble *et al.*, 2012). The slope deposits in these localities mainly result from the degradation of the last interglacial cliff cut in a poorly-consolidated limestone. Therefore, assuming this degradation occurred relatively quickly after the sea regressed, the plains that are today covered by a dry forest might have been wetter when the slope deposits containing *A. patula* formed.

Climatic conditions have also changed significantly, particularly between 8 500-3 000 years BP when the region was considerably wetter than it is today (Hodell *et al.*, 1991; Curtis *et al.*, 2001; Mangini *et al.*, 2007). Throughout the Caribbean region, the shift between this “Holocene moist optimum” and current climatic conditions is characterised by a succession of alternating wet and dry periods marked by short duration events of pronounced aridity, especially during the first millennium CE (Hodell *et al.*, 1995; Malaizé *et al.*, 2011). The fact that the layers of *Cadet 3* containing the most *Amphibulima patula* shells are those which formed during this moist optimum, and that *A. patula* is present before the Holocene arid events at other sites with reliable age estimates for these shells (*Abri Patate*, *grotte du Morne Rita*, and *Pointe des Mangles 2*) supports the hypothesis that variations in both the abundance and distribution of *A. patula* was related

to climatically-driven environmental changes. This is also supported by the association of *A. patula* and *Pleurodonta lychnuchus* in deposits containing fossil shells. This latter species, endemic to Guadeloupe, is known to be restricted to the moist semi-evergreen forests and rainforests of Basse-Terre (Tillier & Tillier, 1985), except for a single specimen from Les Saintes reported by Mazé (1883) that is, however, contested by Bertrand (2001). Tillier & Tillier (1985) have also shown this *P. lychnuchus* to be found in moist to wet forests of Basse-Terre with average rainfall ranging between 2 and 4.5 m per year. The presence of this species in Pleistocene slope deposits and at the base of the *Abri Patate* sequence also suggests that a wetter climate favoured the expansion of *A. patula* on the Guadeloupe Islands. This interpretation implies that both historical and modern find spots correspond to wet localities on limestone islands that functioned as ecological refuges during dry periods.

Mazé (1876) considers the disappearance of *Amphibulima patula* from localities documented in the mid-nineteenth century to result from increasing deforestation and cultivation of the island. Interestingly, both recorded cases of *A. patula* are located at the edge of the *Grands Fonds* area, a hilly sector in the central and western part of Grande-Terre. The marked relief of this area was unsuited to large scale sugar cane cultivation, which played a central role in the economic development of the island from the end of the seventeenth century to the nineteenth century (Lasserre, 1961). The *Grand Fonds* area therefore remained the last region with freely available land for settlement and cultivation to the increasing number of emancipated slaves in the 1830s preceding the abolition of slavery of 1848. The influx of people into the sector and its subsequent cultivation in the form of itinerant gardens at the end of the first half of the nineteenth century corresponds to the precise period when *A. patula* disappears. In geomorphological terms, the practice of slash and burn agriculture and itinerant Creole gardens are known to have evoked substantial environmental changes linked to soil erosion and depletion (Lasserre, 1961), which is consistent with Mazé correlation between changing land use and the disappearance of *A. patula* from Guadeloupe. This author also considers the discovery of *A. patula* on Marie-Galante to be linked to a less extensive cultivation of the island, while recognizing the high probability of snail extirpation that would be caused by future deforestation (Mazé, 1876). This is in agreement with our observation that this locality had been cultivated and the current absence of *A. patula* on Marie-Galante.

With that said, human-induced alteration of the environment cannot be solely responsible for the scarcity or disappearance of *A. patula* on the Guadeloupe Islands. Numerous species of terrestrial molluscs, several endemic, inhabit both the moist and dry forests of the archipelago and are not as rare as *A. patula* (Tillier & Tillier, 1985; Bouchet & Pointier, 1998; Bertrand, 2001). More than seventy terrestrial mollusc species, 45 being natives, have been identified on Guadeloupe islands, with biodiversity

higher in dry and moist semi-evergreen forests than in rainforest (Bertrand, 2001; Charles, 2015). This suggests that the impact of historic-period environmental alteration only moderately influenced the molluscan diversity of the archipelago. The scarcity of *A. patula* on Grande-Terre, and its disappearance in La Désirade and, perhaps, Marie-Galante also involves a natural factor, namely a distribution limited to a small number of ecological refuges during dry periods. Such a distribution precludes any re-colonisation after the snails disappeared as a result of cultivation practices. Therefore, a combination of factors, in this case a limited geographic distribution and a human-driven alteration of the landscape, contribute to the extreme scarcity and high risk of the future disappearance of this species from Guadeloupe.

5 - CONCLUSION

Amphibulima patula was historically known in Guadeloupe from a very small number of stations where it is currently no longer found. Over the last ten years, this species has been observed at a single station on a single occasion, revealing it to be the rarest of all the Guadeloupe land snails

The distribution of fossil specimens does however indicate a wider distribution on Grande-Terre and Marie-Galante in the past, as well as the former occurrence of the species on La Désirade. Dated deposits containing *A. patula* shells support the idea that fluctuations in the distribution of this species result from environmental changes, both locally and climatically-induced.

Changes in past environmental conditions would have resulted in periods when this otherwise extremely rare species significantly expanded its range. Its past distribution is particularly interesting for documenting wetter periods during which the low-lying limestone islands of the Lesser Antilles would have supported a wetter forest than at present-day. Despite its current rarity, *Amphibulima patula* nevertheless represents a useful palaeoenvironmental marker, which, when found in archaeological and geological sites, can help reconstruct the palaeoenvironmental conditions that prevailed during the formation of the deposits.

Finally, the rarity of this snail would therefore reflect its distribution being limited to a few wet areas on limestone islands as a consequence of current arid conditions. This distribution restricted to a few ecological refuges weakened *A. patula* populations which, when combined with human-induced environmental changes, provoked a considerable reduction in its numbers, making *A. patula* a species prone to extirpation on Guadeloupe.

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