DRYMAEUS VIRGULATUS, AN EXTIRPATED LAND SNAIL SPECIES ON SAINT KITTS AND TINTAMARRE ISLANDS

***Drymaeus virgulatus*, una especie de caracol terrestre extirpada en las islas de San Cristóbal y Tintamarre**

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ABSTRACT

The land snail species *Drymaeus virgulatus* (Férussac, 1821) is recorded in St. Kitts in the form of 21 complete or fragmented shells collected on the island in November 2019. The complete shells were collected on the backshores of South Frigate Bay and Majors Bay, while shell fragments come from naturally exposed sections of the North Frigate Bay sand ridge, where they date to the pre-Columbian period. This evidence therefore attests to the past presence of this species on the island. The absence of this taxon from recent malacological surveys points to it having been extirpated from St. Kitts. Apertural fragments of a large bulimulidae collected in the caves of Tintamarre Island, near St. Martin, are also related to this taxon, adding a second West Indian island from which this species apparently disappeared in recent centuries.

Keywords: Terrestrial molluscs, new record, local extinction, St. Kitts & Nevis, Saint Martin.

RESUMEN

La especie de caracol *Drymaeus virgulatus* (Férussac, 1821) se registra en San Cristóbal con 21 conchas enteras o fragmentadas recogidas en la isla en noviembre de 2019. Las conchas completas fueron recogidas en las costas de South Frigate Bay y Majors Bay, mientras que también se han recuperado fragmentos en secciones naturales de la duna costera de North Frigate Bay. Estos últimos materiales están asociados a la época precolombina. Por lo tanto, estos hallazgos atestiguan la presencia pasada de esta especie en la isla. La ausencia de este taxón en los estudios malacológicos recientes lleva a considerar que ha sido extirpado de San Cristóbal. Los fragmentos aperturales de un gran bulimúlido, recogidos en las cuevas de la isla de Tintamarre, cerca de San Martín, también están relacionados con este taxón, lo que añade un segundo ejemplo de isla antillana de la que esta especie pudo haber desaparecido en los últimos siglos.

Palabras clave: moluscos terrestres, nuevo registro, extinción local, San Cristóbal y Nieves, San Martín.

INTRODUCTION

The Lesser Antilles experienced a large number of faunal extinctions since the late Pleistocene, including terrestrial mammals (Cooke *et al.*, 2017), birds (e.g. Pregill *et al.*, 1994; Gala & Lenoble, 2015), chiropterans (e.g. Pregill *et al.*, 1994; Stoetzel *et al.*, 2016), and squamates (e.g. Bailon *et al.*, 2015; Kemp & Hadly, 2016, Bochaton *et al.*, 2019, 2021). It is still unclear, however, whether these disappearances concern uniquely vertebrates or all terrestrial animal species. In fact, little data concerning terrestrial invertebrate fauna is currently available in the Caribbean due to the unlikelihood of this material being preserved in the fossil record. Snails, however, are an exception, as their shells are susceptible to being preserved in fossil deposits.

Notwithstanding this potential, very limited data is currently available for the evolution of terrestrial gastropod communities in the Lesser Antilles. The fossil record, in particular, has been paid little attention by researchers working in this region of the Caribbean despite archaeological sites in the Lesser Antilles yielding significant quantities of terrestrial gastropod shells (Jones, 1985; Serrand, 2005; Stouvenot *et al.*, 2014). Moreover, recovered taxa are very rarely determined to species.

Natural deposits are also likely to produce fossil malacological assemblages. For instance, fossil terrestrial gastropod assemblages from the island of St Eustatius were described based on shells preserved in Holocene paleosols (Van der Valk, 1987). However, this case is quite unique, with the only other example being a recent study of terrestrial gastropod shells collected from caves on Tintamarre Island, near St. Martin (Bochaton *et al.*, 2020). Of interest here, this latter work demonstrated that up to 5 land snail taxa likely disappeared from the island, suggesting that the terrestrial mollusc community is no less sensitive than vertebrate fauna to human-induced environmental changes that shaped the island's terrestrial fauna community over the last several centuries.

This study reports on the past presence of *Drymaeus virgulatus* (Férussac, 1821) on St. Kitts in the form of old shells collected from backshore positions and subfossil specimens from a sand ridge. The absence of these species in recent malacological surveys leads us to consider it as extirpated from the island. While several specimens are represented uniquely by fragmented shells, their size can nevertheless be estimated by comparison with current specimens from the islands of the Anguilla Bank and fossil specimens from a pre-Columbian coastal sand ridge on St. Martin. The past shell size variability of this taxon's therefore appears more important than observed in present-day populations of the northern Lesser Antilles. Comparison of specimens from St. Kitts with fragments of large bulimulidae collected in caves on Tintamarre equally supports the past presence of *Drymaeus virgulatus* on this island.

OBJECTIVES

- Demonstrate the existence of *Drymaeus virgulatus* in the recent and fossil record from the islands of St. Kitts and Tintamarre and the current absence of living populations on these same islands.

MATERIAL AND METHODS

St. Kitts is one of the Leeward Islands in the western chain of the Lesser Antilles (latitude 17.30 N, longitude 62.80 W) which, with the neighbouring island of Nevis, forms the Federation of St. Kitts and Nevis. This elongated island is 176 kilometres long and dominated by a central mountain range, culminating with Mount Liamuiga (1156 m) towards the north. This mountainous area is covered by upland forest surrounded by cane-covered slopes, incised by ghauts that drain into the sea. These slopes are characterised by a vegetation gradient typical of the Lesser Antilles; dry vegetation occupies low rocky hills, and is replaced by mesophytic flora at mid-elevations and rainforest on the highest parts of the mountains (Lindsay & Horwith, 1999). The mountain range extends southward into the southeast peninsula, which is composed of rocky hills below 300 metres and flat sedimentary plains covered with dry scrub woodlands punctuated by ponds. The island of St. Kitts is composed almost entirely of volcanic rocks, with the only calcareous areas being the golden beach and coastal limestone sand ridges that line the bays of the southeast peninsula.

Our current understanding of the terrestrial mollusc fauna of St. Kitts and Nevis is based on two surveys carried out over the last twenty years (Breure *et al.*, 2016); with 26 taxa listed for the terrestrial mollusc community of St. Kitts, this work makes land molluscs from these two islands amongst the best documented in the Lesser Antilles.

Shells were collected from ten stations during a short stay on the island in November 2019. Each collection station was labelled by associating the island code (SKB) with locality number according to the order of collection. The material considered in the current study concerns both whole or fragmented shells of *Drymaeus virgulatus* found during this survey. It comes uniquely from 5 stations on the south-eastern peninsula (Fig. 1). Shell fragments were collected from the first two survey sites; natural sections exposed by the sea in the North Frigate Bay sand ridge (SKB_001: WGS84; 62.672397°W; 17.276348°N) and from sections of a sand extraction trench in the same ridge (SKB_002: 62.673089°W; 17.27621°N). Whole shells were also collected in the coastal forest to the east of South Frigate Bay (SKB_008: 62.672996°W; 17.273266°N) and on the backshore a few hundred metres further west (SKB_010: 62.672397°W; 17.276348°N). Finally, fragments were collected along the edge of the salt pond in the backshore of Major Bay (SKB_009: 62.673967°W; 17.273502°N).

A comparative sample was also assembled comprising some 30 specimens collected in May 2019 as fresh or live specimens on the three main islands of the Anguilla Bank, namely St. Martin (n = 18), St. Barth (n = 5), and Anguilla (n = 7). A series of nine fossil specimens from Saint Martin, collected in the natural sections of the sand ridge of *Etang Rouge* beach, were also included. These sections were exposed during cyclone Inés in 2017. The shells were found in association with *Arca zebra* shells, a little less than one metre above ground level, preserved in a carbonate accumulation horizon of a buried paleosol. *Arca zebra* accumulations preserved in this sand ridge have been reported for the pre-ceramic Amerindian period and date to between 1000 and 3300 BCE, i.e. during the very first millennia of the island's pre-Columbian occupation (Bonnissent *et al.*, 2016).

Three subfossil shell fragments of a large Bulimulidae, collected in May 2019 in the of *Trou de Souris 4* on the island of Tintamarre near Saint Martin and referred to as Bulimulidae *gen et sp indet.* (Bochaton *et al.*, 2020), were also included in the study.

The shells were observed with a Leica binocular magnifier up to 60x magnification, and photographs were taken using a camera equipped with a macro lens mounted on a micrometric slide to permit focus stacking and image reconstruction with the Helicon Focus software. Measurements of shell height (H), shell width (W), aperture height (HA), and aperture width (WA) follow definitions provided by Breure (1974). Measurements were acquired using a digital calliper and recorded to one tenth of a millimetre. The EXCEL software was used to process measurements, establish the linear regression curve, and generate the Pearson coefficient of determination (r^2).

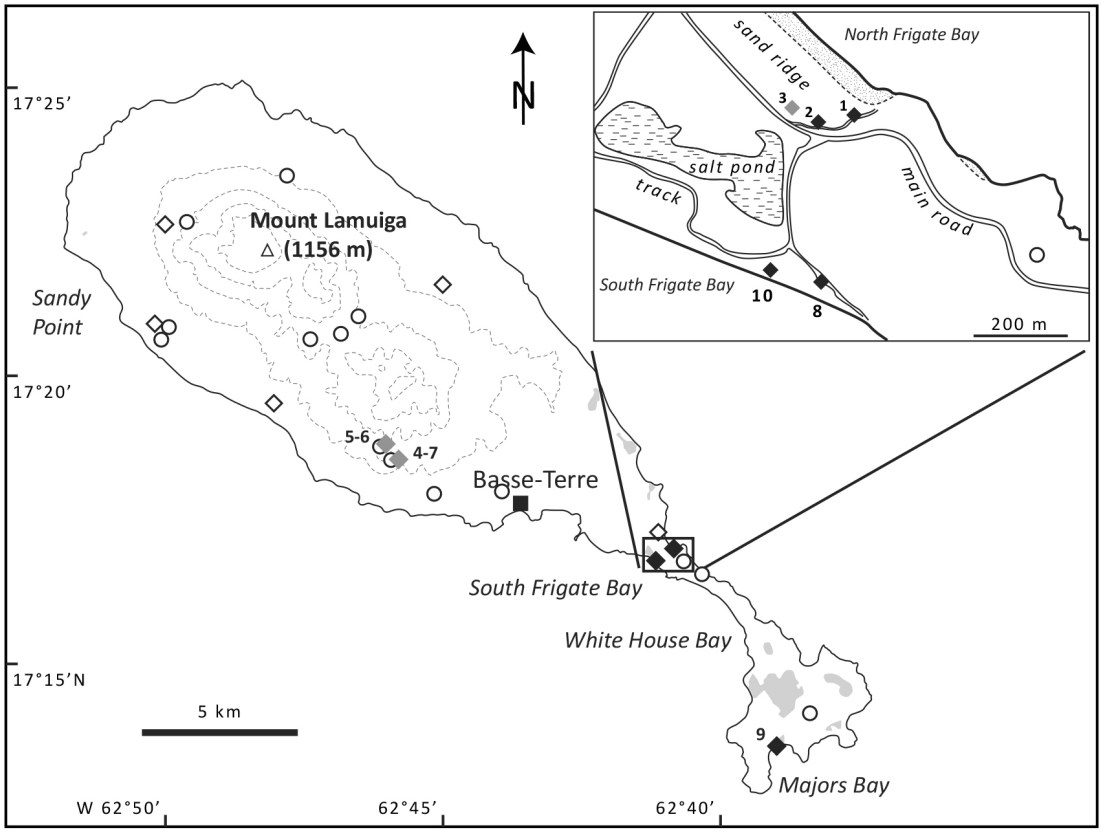

Figure 1. Map of St. Kitts with localities sampled in 2019 (black diamond: locality yielding specimens of *D. virgulatus*; grey diamond: locality devoid of this species) and localities reported by Breure *et al*. (2016) from sampling carried out in 2014 (white diamonds) or in 2004 (white circle). Inset shows the area around Frigate Bay and the locality numbers. Contour lines represent 200 m intervals.

RESULTS

Twenty-one specimens, either whole shells or shell fragments, collected at the 5 sampling localities, are attributed to *Drymaeus virgulatus* (Férussac, 1821), also frequently referred to as *Drymaeus elongatus* (Röding, 1798) in the literature. Whole shells are shown in Fig. 2 and the most complete fragments in Fig. 3.

The three complete shells correspond to juvenile individuals. These specimens were collected from the two localities of Frigate Bay South (SKB_008, n = 2; SKB_010, n = 1). All shells display a fine, regularly reticulated apex of riblets and spiral striae characteristic of the *Drymaeus* genus (Fig. 2B; Pilsbry, 1897−1898). The shells are conical and robust with straight sides and a fairly obtuse apex. The whorls are slightly convex. The ovate aperture is positioned quite obliquely to the shell axis, representing half of the shell's overall height, and displays a reflexed columellar margin extending on to the parietal side. All of these characters are consistent with *Drymaeus virgulatus* following Pilsbry (1899). The palatine side of the aperture is thin and non-reflected, while the last whorl has a pronounced keel. Both characters reflect the juvenile status of these specimens, as also indicated by their moderate size (shell heights of between 14 and 17 mm).

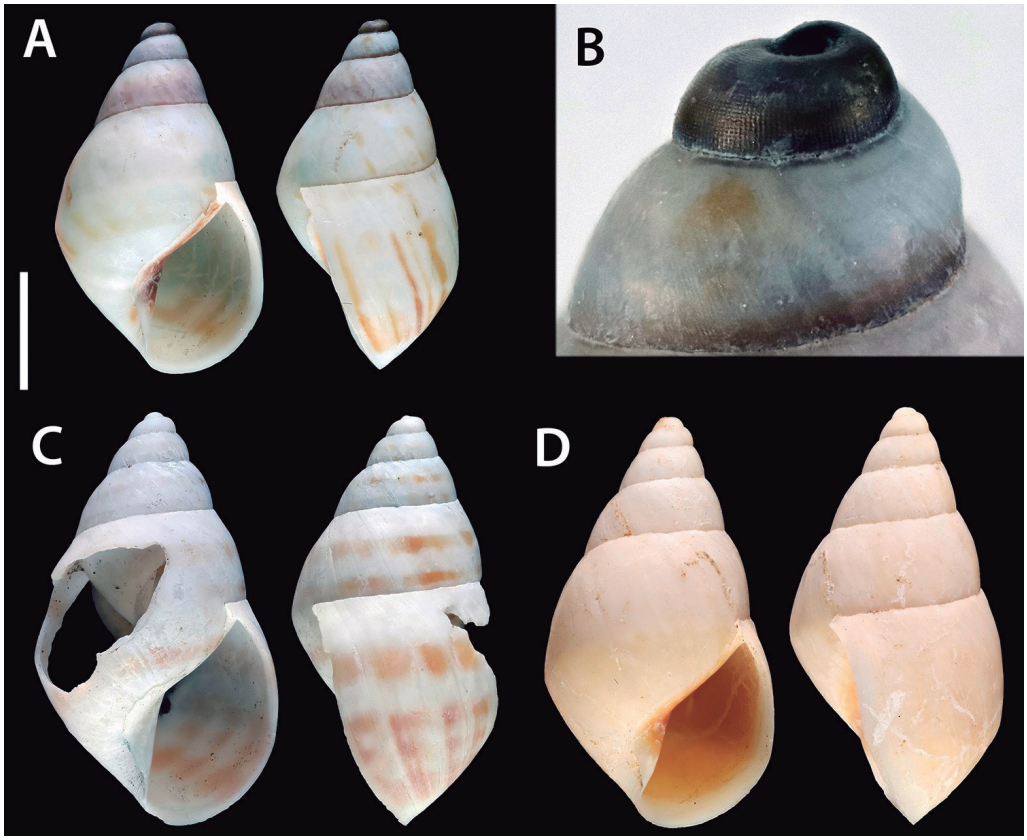

Figure 2. Whole shells of *Drymaeus virgulatus* collected from localities SKB_008 (A, C) and SKB_010 (D), and view of the protoconque of one specimen collected from locality SKB_008 (B). The scale bar represents 5 mm.

The species *Drymaeus virgulatus* is known for being a variable species of this genus, with several varieties distinguished according to their colour pattern (Pilsbry, 1899; Baker, 1924), as illustrated by several modern specimens from the Anguilla Bank (Fig. 4). The specimens from St. Kitts include several varieties. The apical whorls of the first specimen are dark bluish, similar to the blue tipped-form reported by Pilsbry (1899), with the last whorls decorated with brown axial bands (Fig. 2A). The second specimen displays discontinuous axial bands formed of lines of light brownish red dots sometimes flammulated by spirally arranged blotches of colour (Fig. 2C), similar to the spirally-banded type of Baker (1924). The last specimen is uniformly beige, with an internally coloured brown columella (Fig. 2D), rendering it similar in these characteristics to the "typical" variety identified by Pilsbry (1899).

The shell fragments are most often represented by the last whorl, as fractures followed the suture between the last and penultimate whorls. This last whorl may be complete or partial. In all cases, these fragments are attributed to *D. virgulatus* based on the morphology of the opening, which is elliptical and high with vertical or subvertical columella, a slightly convex parietal edge of the aperture, an expanded basal side and, in most cases, a slightly (Fig. 3A, B, E) or heavily faded (Fig. 3C, F) colouration of the spiral band pattern.

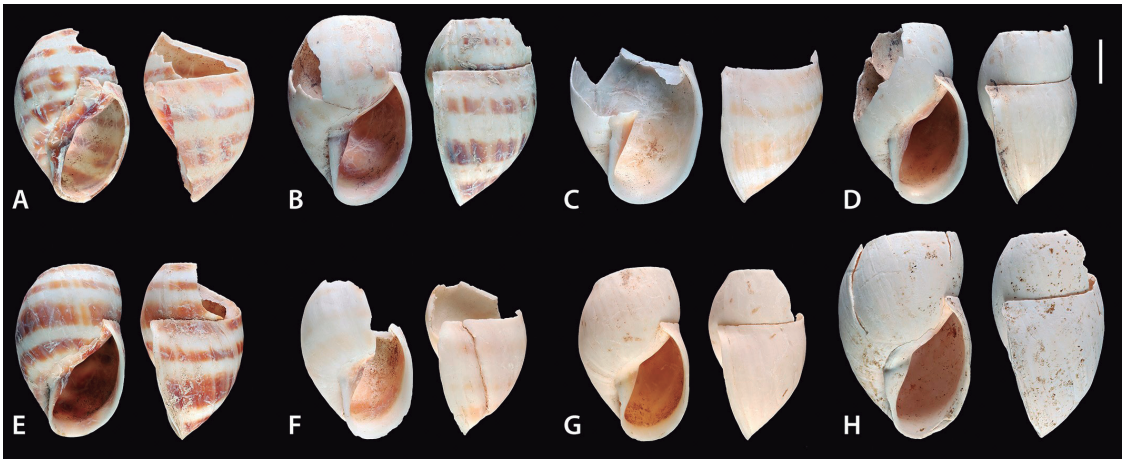

Figure 3. Fragments of *Drymaeus virgulatus* shell collected from localities SKB_001 (A), SKB_002 (B-D), and SKB_009 (E-H). The scale bare represents 5 mm.

While certain specimens are coloured, none as brightly as the fresh specimens collected from the different islands of the Anguilla Bank. The blurred character of the colouring combined with the presence of concretions or signs of dissolution supports the shells being old.

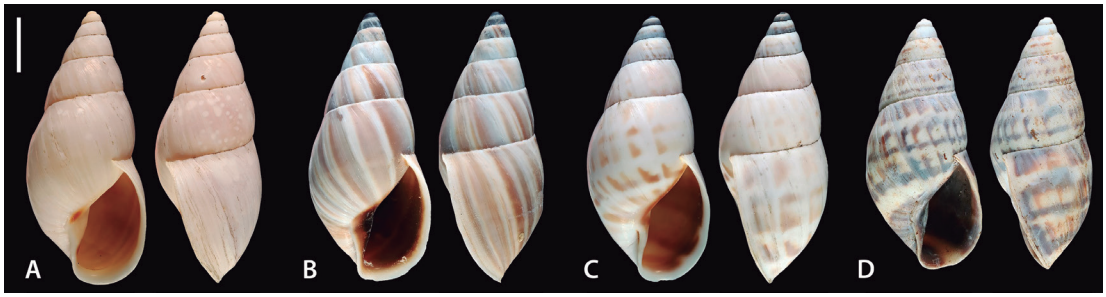

Figure 4. Modern *Drymaeus virgulatus* shells collected on St. Barth (A, C) and St. Martin (B, D) illustrating the variable colouring pattern of the species. The scale bare represents 5 mm.

Compared to specimens from the Anguilla Bank, shells from St. Kitts display a relatively larger aperture width, which results in a larger shell width for the same opening height. However, when specimens complete enough to allow these two measurements are plotted alongside current specimens from the Anguilla Bank, this difference falls within the overall variability of the species (Fig. 5A), especially given that specimens from the Anguilla Bank have long been known to have a narrow aperture (Pilsbry, 1899).

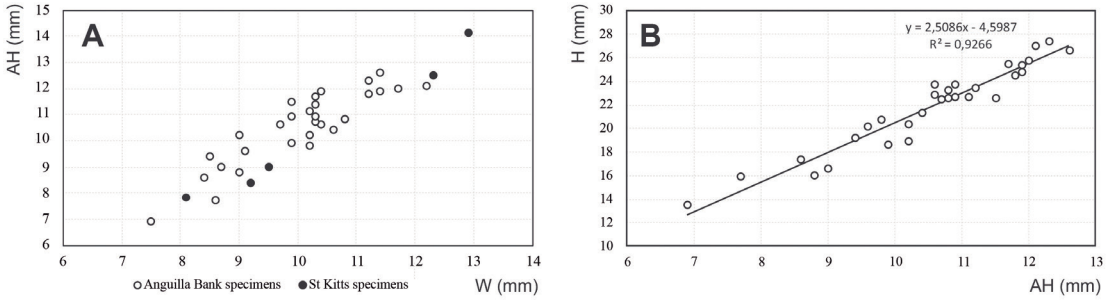

Figure 5. Metric of *Drymaeus virgulatus* shells. A, bivariate plot showing the aperture height (AH) and shell width (W) of current *Drymaeus virgulatus* from the Anguilla bank islands relative to St. Kitts specimens. B, linear regression curve between shell height (H) and aperture height (AH) in modern specimens of *D. virgulatus* from the Anguilla Bank.

In order to have a more substantial sample to appreciate the height of the shells of the St Kitts specimens, the shell height of fragmented specimens was estimated based on aperture height. For this purpose, the correlation between these two measurements was established using fresh specimens from the different islands of the Anguilla Bank (Fig. 5B). The correlation curve was then used to estimate the height of eleven fragments complete enough to allow aperture height to be measured. Estimated heights and measurements taken on complete shells demonstrate specimens to range in size from 14.4 mm for the smallest (Fig. 2A) to 32.8 mm for the largest (Fig. 3H). These measurements are in good agreement with the reported dimensions for this species; 33 mm shell height for the largest specimens of Saint Croix (Pilsbry, 1899) and 32.2 mm for those from the ABC Islands (Baker, 1924).

Interestingly, several of the St. Kitts specimens are larger than those in the comparison sample (Fig. 6). The current specimens from the islands of the Anguilla Bank we collected do not exceed 27.4 mm, and the fossil specimens from St. Martin have an estimated maximum height of 27.8 mm, while 3 of the 11 fragments collected from St. Kitts have an estimated height approaching or exceeding 30 mm.

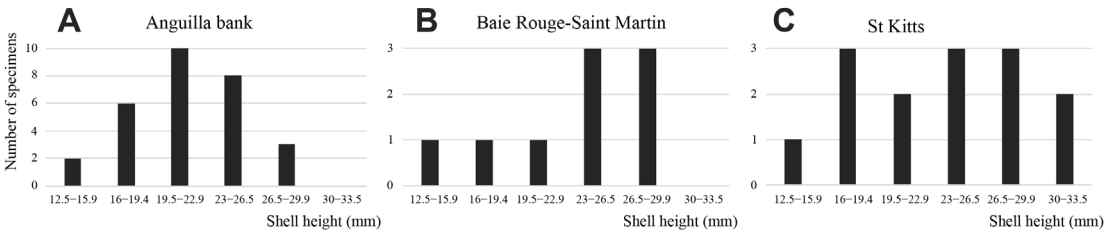

Figure 6. Histograms of shell height. A, current specimens from the islands of the Anguilla Bank. B, fossil specimens from St. Martin. C, old and subfossil specimens from St. Kitts.

Finally, 3 shell fragments of large bulimulidae collected in the cave of the *Trou de Souris 4* on Tintamarre Island were re-examined. These specimens correspond to apertural fragments of the last whorl, as illustrated by the largest fragment (Fig. 7), and are all of comparable size. The slightly convex palatal edge of the opening, the recurving of this edge at the junction with the last whorl, and a reflexed and flattened basal edge makes these specimens similar to our *D. virgulatus* specimens. The height of the opening can be estimated at 13.8 mm for the largest fragment, which correlates with a shell height estimate for the specimen of a little over 29 mm. In addition, this specimen preserves a coloration of brown axial bands becoming more pronounced downward (Fig. 7), a pattern comparable to one of our shells from St. Kitts (Fig. 2A) or modern specimen from the Anguilla bank (Fig. 4B). Despite the fragmented nature of the shells, they are referred to *Drymaeus virgulatus* based on the morphological characteristics of the three fragments and the colour pattern preserved by one of the specimens.

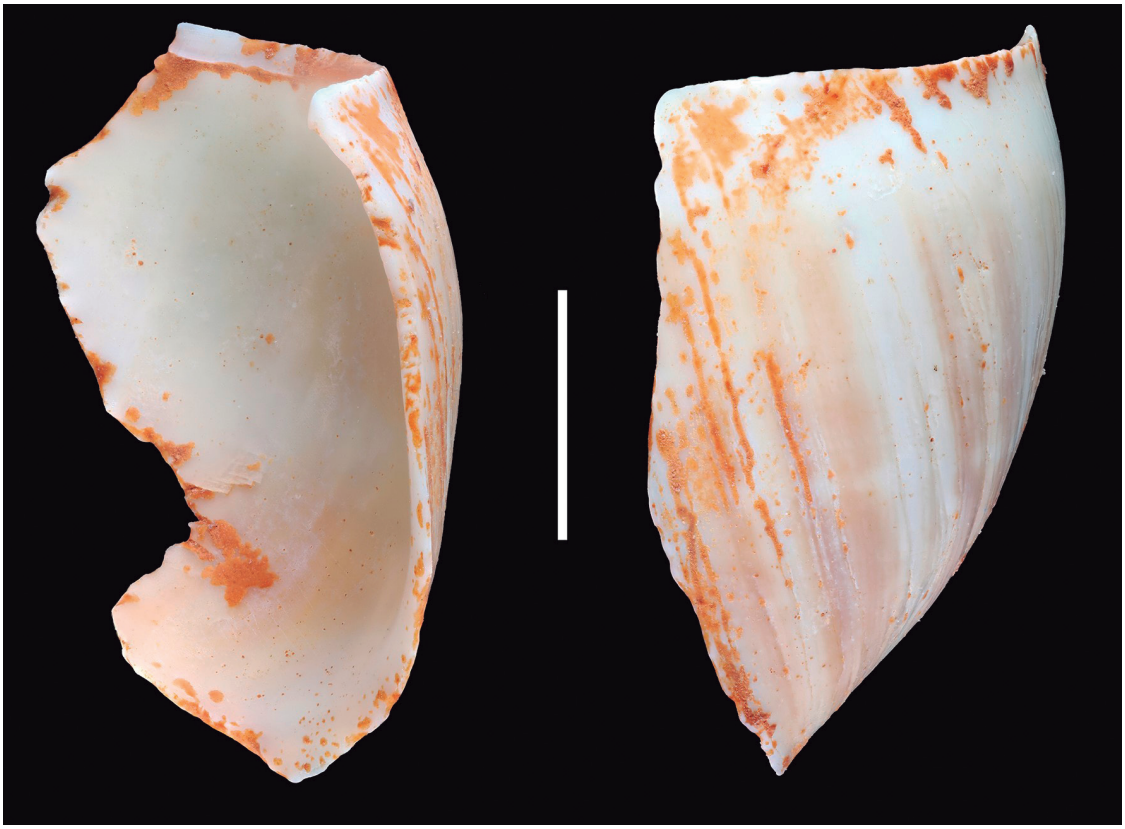

Figure 7. Apertural fragment of the bulimulidae specimen from Trou de Souris 4, on Tintamarre in apertural (left) and lateral (right view), referred here to *Drymaeus virgulatus*. The scale bare represents 5 mm.

DISCUSSION

The specimens collected on St. Kitts can be reliably referred to *Drymaeus* based on a combination of the sculpture of the apical whorls for whole shells, the morphology of the shell and aperture, shell size, and the colouring patterns for whole and fragmented shells. These specimens thus attest to the presence of old shells of this taxon in several localities on the southeast peninsula, adding a twenty-seventh taxon to the list of the island's terrestrial molluscs.

In addition, the comparative material used, particularly specimens from paleosols preserved in the Baie-Rouge sand ridge, attest to the presence of this taxon from the earliest moments of the pre-Columbian occupation of Saint Martin, while our re-examination of bulimulidae *gen. et sp. indet* fragments from the caves of Tintamarre provides evidence for the presence of *D. virgulatus* on this island from which it is now absent.

To date, *Drymaeus virgulatus* was considered a dubious taxon or erroneously reported from St. Kitts, and consequently removed from the island's faunal list (Breure *et al.*, 2016). The assumption of its previous presence on St. Kitts was based on Pilsbry's 1899 report of *Drymaeus liliaceus*, accepted as being synonymous with *D. virgulatus* by Breure *et al*. (2016). Neither of these two surveys of the island's mollusc fauna carried out over the last twenty years produced evidence for the presence of this taxon despite sampling being carried out at 25 localities, 4 of which were located on the southeast peninsula (Breure *et al.*, 2016).

The recovery of *D. virgulatus* specimens at 5 of our sampling localities can be explained by the fact we looked for material buried in sand ridges and collected immature specimens and fragments, which are usually overlooked in malacological surveys. Our recovery these specimens is equally due to the fact that we surveyed backshores, which are favourable places for the collection of old material exposed by erosion or accumulated by storms (Fitzpatrick, 2010), but which are otherwise of very little malacological interest. No live specimens or fresh shells were recovered during our surveys. Moreover, the absence of *D. virgulatus* specimens in recent surveys supports this species having been extirpated from the island.

Unburied shells are difficult to date; their colouration, however, can be preserved over long periods in favourable conditions as its carried by the mineral component of the shell and not only the periostracum. For example, Pfeiffer (1856) described *Bulimus extinctus,* the Pleistocene form of *Drymaeus virgulatus* from St. Croix, based on a shell with a preserved colour pattern ("brown spots on the shell"). On the other hand, a broad age estimate is possible for the specimens recovered from the exposed sections of the North Frigate Bay sand ridge. The formation of these sand ridges implies that the sea level was close to its current position, suggesting an age no older then the mid-Holocene, when global sea levels stabilised, approaching their present-day position (Khan *et al.*, 2017). Moreover, archaeological excavations in the Caribbean have shown that shell remains buried in such ridges are generally between half a millennium to a few thousand years old (Bertran, 2012; Guibert *et al.*, 2017; Lopez, 2019), and thus related to the Amerindian occupation of the islands. In the Lesser Antilles, this period spans from 6000 to 500 years before present (Napolitano *et al.*, 2019). It can therefore be assumed that the fragments collected in North Frigate Bay attest to the past presence of *D. virgulatus* on the island during the pre-Columbian period. This assumption can be confirmed by additional research including the implementation of a precise dating program, which is however beyond the scope of this work.

The distribution of *Drymaeus virgulatus* is Caribbean, including the islands of Hispaniola (Espinosa & Robinson, 2021), Puerto Rico (Van der Schalie, 1948), the British and American Virgin Islands (Pilsbry, 1899), the islands of Anguilla Bank (Hovestadt & Neckheim, 2020), St. Eustatius (Van Leeuwen & Hewitt, 2016), Antigua (Pilsbry & Brown, 1914), and the ABC Islands (Hovestadt & van Leeuwen, 2017). The identification of the taxon on St. Kitts indicates that the distribution of this taxon was more widespread than it is today, extending southward in the Lesser Antilles as far as St. Kitts, if not further. For example, the species was mentioned as occurring on Guadeloupe by Mazé (1883) in the second half of the 19th century and has not been reported during recent surveys (Bouchet & Pointier, 1998; Bertrand, 2001; Charles, 2015), leading to questions being posed as to the reliability of the mention (Charles, 2015) or even a possible error in the reported locality (Bertrand, 2001). However, it is also possible that this species was present in the past and has now been extirpated from Guadeloupe, similar to the case of St. Kitts. The latter hypothesis is supported by the observation that the site from which the specimen was collected in the 19th century (i.e. the beach of the slave cemetery at Le Moule, now known as *Plage de l'Autre Bord*) was intensively developed in the second half of the 20th century. Finally, similarly to St. Kitts, Pilsbry (1899) reported *D. liliaceus* on Dominica, where it is absent today (Robinson *et al.*, 2009). The finding of shells of *D. virgulatus* on St. Kitts thus raises questions concerning the potential past presence of this taxon in both Guadeloupe and Dominica and, more broadly, the entire central part of the Lesser Antilles. Additional data is, however, still needed to explore this possibility, for example, by determining the species represented by snail shells collected during archaeological excavations.

The land snail *Drymaeus virgulatus* is an arboreal species typically found in dry coastal environments (Mazé, 1890; Van Buurt, 2016). These already particularly fragile environments were also the first to be settled and exploited during the colonial period (Watts, 1987). The combination of these factors ultimately led to the destruction of most of the dry forests in the West Indies (Lugo *et al.*, 1981). In St. Kitts, the extent of historical exploitation of the low-lying parts of the island, which could potentially host dry forests, precluded the preservation of any patch of the original forest (Beard, 1949). This interpretation is further supported by Van Buurt's (2016) report of a close relationship between *D. virgulatus* and a limited number of plant species, especially *Guaiacum officinale*, a tree of the Caribbean dry forest that was once well represented on the island (Lindsay & Horwith, 1999) and is now absent from St. Kitts (Barstow, 2019). The disappearance of this tree species on which *D. virgulatus* depended from the island's dry forests is thus sufficient to explain the extirpation of the snail. It therefore appears highly likely that the historical transformation of this environment to be the root cause of the extirpation of *D. virgulatus*. The chronological resolution for this species' past presence on St. Kitts is still too imprecise to reliably test this hypothesis. Future work that incorporates material from archaeological excavations should allow the impact of environmental changes on this species to be better evaluated. In addition, the timing of these historic period human-induced environmental changes equally fit with their being responsible for the extirpation of *D. virgulatus* from Guadeloupe. It is also consistent with the possible past presence of the snail on Tintamarre Island, where the disappearance of multiple invertebrate and vertebrate species has been interpreted as resulting from the historical exploitation of the island (Bochaton *et al.*, 2020).

Finally, our results provide only limited insights concerning large specimens (shell heights greater than 29−30 mm), represented by subfossil fragments from St. Kitts. These large specimens are, however, absent from the sample of fresh specimens from the islands of the Anguilla Bank. One potential explanation is that this difference in size reflects population-level variation between the different islands. For instance, Baker (1924: 82) reported differences in size between collections from the different islands of the Netherlands Antilles. According to this hypothesis, *D. virgulatus* would be smaller on the islands of the Anguilla Bank compared to those from St. Kitts. However, the large size of the specimens collected from Tintamarre is inconsistent with this hypothesis. This would support differences in size reflecting another phenomenon, for example, diachronic variation in snail size. Such variations are well known (Goodfriend, 1986). Moreover, the form *Drymaeus extinctus* from the Pleistocene deposits of St. Croix, first named by Pfeiffer (1856) and later synonymized with *D. virgulatus* by Pilsbry (1899), is characterized by their large size. The presence of large specimens in St. Kitts and their current absence from the islands of the Anguilla Bank would argue in favour of the reduction in the shell size of *D. virgulatus* populations over time. This phenomenon of size reduction has previously been reported for *Pleurodonte lucerna* populations in Jamaica, which Goodfriend (1987) described for the last two millennia as being related to climate change. However, multiple factors can induce population-level variations in shell size (Goodfriend, 1986). As the morphological response of terrestrial gastropods to environmental variations is species specific (Goodfriend, 1992), an expanded database of *D. virgulatus* specimens is necessary to test this. In this respect, the integration of fossil and archaeological material is of primary interest for further exploring this question.

ACKNOWLEDGMENTS

This study was conducted as a part of the ECSIT Project of the CNRS with a financial support from the European PO-FEDER program (grant no. 2016-FED-503), the Guadeloupe Regional Council, the DAC of Guadeloupe (PCR Extinctions), and the CNRS (SEEG ECSIT). The author thanks Thomas Cojon, who cleaned the field samples, Anna Ruffa, who kindly edited the Spanish summary, Brad Gravina for English language editing, and Laurent Charles and Bram Breure for their constructive comments and suggestions.

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[Recibido: 24 de febrero, 2021. Aceptado para publicación: 29 de mayo, 2021]