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Cone snails on the North-Western Cabo Verde Islands: contribution to their ecology

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RESUMO

Os caracóis marinhos (família Conidae) são um dos grupos mais abundantes de invertebrados marinhos vivos e um contribuinte essencial para a biodiversidade marinha. Os caracóis marinhos são encontrados comumente e amplamente distribuídos por todas as áreas tropicais dos oceanos. São espécies com deslocação muito lenta que normalmente ficam no mesmo local grande parte da vida. O habitat mais comum destes caramujos ocorre nas margens dos recifes de coral. Em Cabo Verde, vários atributos observados das populações estão de acordo com as expectativas de um modelo de características ecológicas de pedras, areias e recifes proposto por Rolán (2005). Embora estudos importantes confirmem a diversidade, origem e distribuição com base na filogenia molecular dos caracóis marinhos de Cabo Verde, o habitat e a ecologia básica destes permanecem pouco compreendidos, principalmente nas ilhas do noroeste. Neste trabalho, amostrámos várias novas áreas, analisámos características morfológicas e o habitat dos caracóis marinhos. A morfologia dos habitats é variada. No entanto, a adaptação a novos habitats parece promissora. Neste trabalho, propomos quatro diferentes tipos de habitat para os caracóis marinhos de Cabo Verde nas ilhas do noroeste, onde incluímos dois novos habitats, em contraste com o observado noutras ilhas do arquipélago.

Palavras-chave: *Africonus, Conus*, endémico, habitat, marinho

ABSTRACT

Cone snails (family Conidae) are one of the most abundant groups of living marine invertebrates, and an essential contributor to biodiversity in the sea. Cone snails are commonly found and extensively distributed throughout all tropical oceans. They are very slow-moving species that typically stay in the same location for most of their lifetime. Their most common habitat occurs on fringing coral reefs. In Cabo Verde, several attributes of the observed populations conform to expectations of a model of ecological characteristics of stones, sands, and reef proposed by Rolán (2005). Although significant studies confirm the diversity, origin, and distribution based on molecular phylogeny of the Cabo Verde cone snails, their habitat and basic ecology remain poorly understood, mainly in the north-western islands. In this study, we sampled various new areas, analysed morphological characteristics of cone snails and their habitat. The morphology of the habitats is varied. However, adaptation to new habitats looks promising. In this work, we propose four types of habitat for Cabo Verde cone snails in the north-western islands, where we include two new habitats, in contrast to what was observed in other islands of the archipelago.

Keywords: *Africonus*, *Conus*, endemic, habitat, marine

INTRODUCTION

Cone snails are tropical marine gastropods belonging to the Conidae family (superfamily Conoidea). Recent literature has suggested the existence of approximately ~800 living species (Olivera *et al.* 2014, Puillandre *et al.* 2014, Tenorio *et al.* 2020). Cone snails are among the most abundant groups of living marine invertebrates and an essential contributor to biodiversity in the marine realm, commonly found and extensively distributed throughout all tropical oceans (Duda & Kohn 2005). They are very slow-moving, typically inhabiting the same location for most of their lifetime. They can be classified based on their primary prey (Puillandre *et al.* 2012, 2014): the vermivorous species that eat polychaetes, hemichordates, and echiuroid worms (worm-hunters), molluscivorous species that hunt other mollusks (snail hunters), or piscivorous (fish hunters). The endemic cone snails in Cabo Verde are vermivorous, considering their radula (Cunha *et al.* 2005).

The Cabo Verde Archipelago is a cone snail hotspot in the Atlantic Ocean with 52 mostly stable species, of which 49 are endemic – a much higher diversity than anywhere else in the Atlantic Ocean (Monteiro *et al.* 2004, Duda & Rolán 2005, Rólan 2005, Khon *et al.* 2014). In Cabo Verde, the great variety of cone snail species represents about 10% of the global species diversity (Monteiro *et al.* 2004). The species considering in this study are not treated in a taxonomically consistent manner in the literature. Considering the recently reconstructed phylogeny, the analysed species in this work belong to the *Africonus* subgenus, sister taxa to *Lautoconus* (Abalde *et al.* 2017, Tenorio *et al.* 2020).

Rólan (2005) performed the first comprehensive work in Cabo Verde cone snails. The significant numbers of endemic species are consistent with an independent colonization event by 'small-shelled' and 'large-shelled' cone snail lineages (Cunha *et al.* 2005). Although a significant number of studies confirm the diversity, origin, and distribution of cone snails based on molecular phylogeny (Abalde *et al.* 2017, Cunha *et al.* 2005, Manuel *et al.* 2017), their basic ecology, such as the essential habitats, remains poorly understood.

The Cabo Verde Islands (Fig. 1) were formed by rock accumulation from volcanic eruptions, and they are located in the eastern central Atlantic, around 570 km from the West African coast. Cabo Verde is rocky underwater and covered by several reef organisms referred to as coralline community (Almeida *et al.* 2007). The north-western islands of Santo Antão, São Vicente, and Santa Luzia (the latter is a marine reserve) are located on the second largest insular shelf of Cabo Verde, one of the areas with the richest marine biodiversity in the archipelago (Almeida *et al*. 2015, Freitas *et al.* 2015), also for cone snails (Duda & Kohn 2005). The cliffs and rocky areas on the northern and north-eastern regions are exposed to constant wave action, especially on Santa Luzia. The southern and south-western areas of those latter islands are mostly flat. They have beaches and sandy bottoms, as well as rhodolith beds which are partially covered in the sub-tidal zone (Freitas *et al.* 2015), thus with more areas suitable for the occurrence of cone snails (Rólan 2005). For this reason, we have chosen those islands to perform a study on the habitat characterization for Cabo Verdean snails. The objectives of this work were: (i) characterize the habitat and (ii) contribute to reshaping the spatial distributions of the cone snails in the North-Western Islands of Cabo Verde.

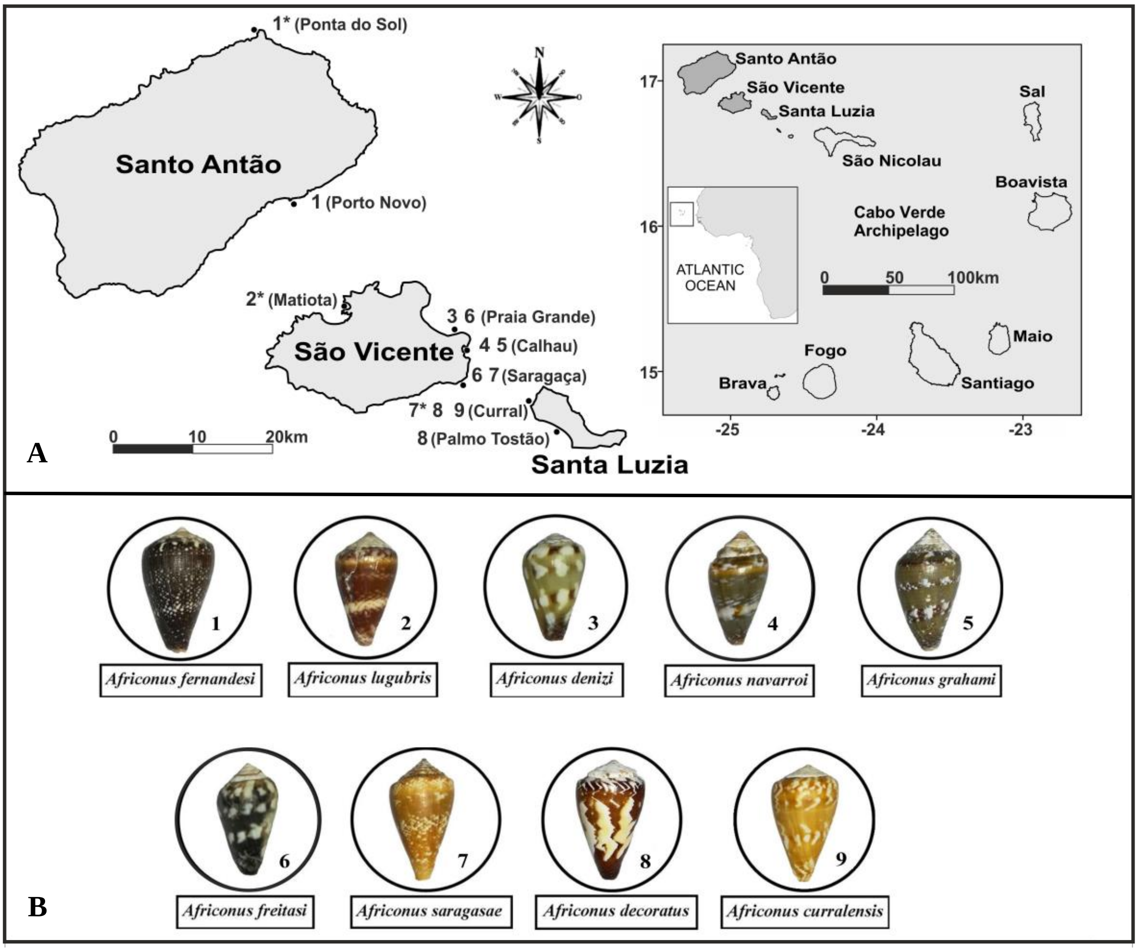

Fig. 1. Sampling sites and sampled species. **A)** Sites on the North-Western Islands in the Cabo Verde Archipelago (marked in grey on the right) where sampling took place are marked in parentheses. **B)** Sampled species. The figures correspond to the species found in each site, also detailed in Table 1. The numbers marked with an asterisk correspond to records of empty shells of cone snail species. Check Results for further details.

MATERIAL AND METHODS

The field studies routines here were made during several scientific expeditions on the North-Western Islands of Cabo Verde (Fig. 1): Santo Antão (Porto Novo and Ponta do Sol), São Vicente (Laginha, Salamansa, Praia Grande, Calhau, Saragaça and Fateja bay) and Santa Luzia (Água doce, Curral, Palmo Tostão beach, nearby Zinho Islet, Portinho, Francisca beach, Praia dos Achados beach and Gurajona bay), from May 2016 to July 2018. The collection of cone snail samples was mostly performed through snorkelling dives (in the evening), from May to July in 2016 and 2017, in small and shallow water bays. During the dives, we searched for the cone snails under rocks, between rock cracks, half-buried in the sand, and between corals or algae. A total of 134 shells samples were collected during several expeditions and included in the present work. Most shells were collected during dive sampling. Specimens that were found alive in the wild were measured and identified *in situ* and then returned to their natural habitat, with only one specimen kept alive for genetic work, according to the recommendation of Tenorio *et al.* (2017).

For the description of the shells, their shape and sculpture were firstly used, followed by the same morphological variables) as Röckel *et al.* (1995), and Tenorio *et al.* (2017). Other morphologic data was retrieved from Tenorio *et al.* (2017), such as data of *Africonus freitasi*, *Africonus miruchae*, and *Africonus denisi*, and compared with our specimens and the specimens from the reference collection on cone snails of the Technical University of the Atlantic (UTA) in Mindelo, Cabo Verde, for species identification. The colouration patterns presented by each species have been described based on the way pigments are deposited, depending on the shape and size of each shell.

The cone snail habitats were characterized according to their physical aspect, the presence of surrounding organisms identified during the dives (free and SCUBA) and photos taken underwater. We described the surveyed habitats based on their surface geomorphological features and the model habitat classifications for cone snails proposed by Kohn & Nybakken (1975).

RESULTS

The results of the morphological traits (shell sizes and pattern) of cone snail species (Table 1), their distribution (Fig. 1 and Table 2), and habitat characterization (Fig. 2) are presented in the following paragraphs.

All the nine cone snail species found in our sampling belong to the *Africonus* clade and belong to the small-shelled species, based on the Cunha *et al.* (2005) classification, as cone snail individual sizes presented maximum shell lengths below 29 mm (Table 1). These cone snails were found in the three studied islands (Table 2) in sites with similar morphological characteristics but with different physiological features. The observations made from field and photo records led to the classification of four habitat types for cone snails, depicted and characterized in Fig. 2.

Table 1. Studied cone snail species. The minimum, maximum, average, and standard deviations values of each shell morphology variables (SL, maximum shell length; MD, maximum diameter; AH, aperture height; SH, spire height; MDH, MD height; PMD, relative position of maximum diameter; RD, relative diameter; RSH, relative SH; all in mm) for each species are presented (in mm; n stands for the number of specimens). Standard colouration patterns (shell) are also depicted.

Species		SL	MD	AH	SH	MDH	PMD	RD	RSH	Shell
1. *Africonus fernandesi* (n= 12)	Average	21.79	13.93	19.28	3.73	17.97	0.93	0.72	0.17	
	SD	2.24	1.51	1.68	0.75	1.66	0.06	0.04	0.02	
	Maximum	25.80	16.70	21.50	3.90	19.60	0.97	0.80	0.19	
	Minimum	18.70	12.80	17.50	2.10	15.20	0.76	0.67	0.11	
2. *Africonus lugubris* (n= 8)	Average	19.80	11.55	15.44	3.76	16.04	1.06	0.77	0.19	
	SD	4.78	2.83	4.83	0.94	4.00	0.17	0.14	0.03	
	Maximum	26.60	15.60	22.40	5.20	21.40	1.34	1.03	0.23	
	Minimum	12.80	7.30	10.10	2.40	10.20	0.96	0.67	0.15	
3. *Africonus denizi* (n=27)	Average	11.62	6.80	9.90	2.25	9.38	0.95	0.68	0.19	
	SD	1.41	0.87	1.25	0.46	1.23	0.05	0.02	0.03	
	Maximum	13.80	8.10	11.90	3.00	11.20	1.00	0.74	0.28	
	Minimum	9.00	5.30	7.90	1.50	7.40	0.85	0.63	0.15	
4. *Africonus navarroi* (n=22)	Average	12.89	7.05	10.62	3.69	9.20	0.87	0.67	0.29	
	SD	2.97	1.67	2.57	0.91	2.25	0.08	0.03	0.04	
	Maximum	18.30	9.60	14.70	6.10	12.70	1.01	0.75	0.36	
	Minimum	8.00	4.40	6.50	2.30	5.70	0.57	0.61	0.21	
5. *Africonus grahami* (n=27)	Average	22.16	11.89	18.33	5.07	17.10	0.93	0.65	0.23	
	SD	2.56	1.71	2.31	0.71	2.28	0.03	0.03	0.03	
	Maximum	27.10	16.00	22.60	6.30	21.20	0.98	0.74	0.29	
	Minimum	16.30	8.60	13.80	3.50	12.80	0.87	0.58	0.17	
6. *Africonus freitasi* (n= 13)	Average	12.73	7.22	10.72	2.02	10.72	1.00	0.67	0.16	
	SD	1.59	1.22	1.44	0.36	1.44	0.00	0.03	0.03	
	Maximum	15.90	9.60	13.70	2.70	13.70	1.00	0.71	0.21	
	Minimum	10.80	5.60	8.80	1.40	8.80	1.00	0.60	0.13	
7. *Africonus saragasae* (n=2)	Average	20.35	9.45	16.90	3.55	16.95	1.01	0.57	0.18	
	SD	0.21	2.05	1.27	0.64	0.64	0.04	0.16	0.04	
	Maximum	20.50	10.90	17.80	4.00	17.40	1.03	0.68	0.20	
	Minimum	20.20	8.00	16.00	3.10	16.50	0.98	0.45	0.15	
8. *Africonus decoratus* (n= 10)	Average	23.30	13.41	19.81	3.87	19.41	0.99	0.68	0.17	
	SD	3.11	2.23	3.18	1.24	2.48	0.06	0.03	0.05	
	Maximum	28.20	16.80	24.10	5.50	23.50	1.09	0.75	0.24	
	Minimum	18.70	10.40	16.00	2.10	16.60	0.92	0.63	0.09	
9. *Africonus curralensis* (n= 13)	Average	16.98	9.87	14.80	1.80	15.18	1.08	0.69	0.10	
	SD	1.93	1.15	1.80	0.72	1.52	0.03	0.03	0.04	
	Maximum	20.20	11.50	17.70	3.10	17.70	1.09	0.71	0.16	
	Minimum	10.80	5.10	9.00	0.50	9.30	0.99	0.57	0.04	

Fig. 2. Habitat types studied, organized in four types. **A)** Type I habitats have an extensive area of corals (most are of *Zoanthus* species) with a skinny 2 m-layer of sand in the cracks. **B)** Type II habitats present a high abundance of algae at about 2–5 m deep, small coralline communities that vary widely in substrate types from complex living coral substrates to dead coral zones, and boulders, with a skinny layer of sand. **C)** Type III habitats are predominantly filled with stones surrounded by a thin layer of sand, covered with a thin layer of algae, few crusted corals, and harbouring many organisms mostly shells and polychaetes (1–2 m). **D)** Type IV habitats are typical on the beach areas with stones and large slabs with brown and green algae, and located in areas of constant wave breaking, and of few centimetres of depth. Check Table 2 to complement the information regarding their location and the cone snails found in each habitat type.

Table 2. Summary of cone snail habitat types, their location, and recorded species.

Habitat	Island and locality	Species
Type I	São Vicente, Laginha	*Africonus lugubris*
Type II	Santa Luzia, Curral and Zinho Islet	*Africonus decorates*
		Africonus curralensis
		Africonus saragasae
Type III	São Vicente, Calhau	*Africonus grahami*
		Africonus navarroi
Type IV	São Vicente, Praia Grande	*Africonus freitasi*
		Africonus denizi
		Africonus fernandesi
	Santo Antão, Porto Novo	*Africonus fernandesi*
	Santo Antão, Ponta do Sol	*Africonus fernandesi*

On Santo Antão Island, the *Africonus fernandesi* specimens were collected in Porto Novo about 2–4 meters deep, in a small, sheltered bay (Fig. 1). Snorkelling in Ponta do Sol (Fig. 1) we also found six well-preserved shells of this species in a habitat remarkably similar to that of Porto Novo (habitat type IV, Fig. 1), which should be considered as a possible new record for *A. fernandesi*. Most of the species distributed in the east of São Vicente Island, namely *A. navarroi*, *A. freitasi* and *A. grahami*, were found on shores of Praia

Grande and Saragaça beach. However, Calhau was the site with a higher density of cone snails (Fig. 1 and Table 2). On this island, we also found only shells of *A. lugubris* (Fig. 1 and Table 2). On Santa Luzia, we found and collected a shell of a specimen of *Africonus curralensis* and two of *Africonus saragasae* (Fig. 1 and Table 2).

DISCUSSION

Most of the endemic cone snails of São Vicente Island (*Africonus navarroi*, *Africonus grahami*, *A. freitasi*, *Africonus saragasae*, *Africonus denizi*, and *Africonus lugubris*) are known to be distributed on the eastern shores (Tenorio *et al.* 2017). Only one endemic species has been described in the northern sites between Matiota (Porto Grande bay) and Salamansa Bay, *Africonus lugubris*, which according to IUCN has not been found alive since 1980, hence considered as presumable Extinct (Peters *et al.* 2016). Of the species known to occur in the eastern shores, we found live specimens of *A. navarroi*, *A. grahami*, *A. freitasi* and *A. denizi*, as it is challenging to find cone snails without extensive and lengthy fieldwork. Regarding the species occurring on Santo Antão, according to Tenorio *et al.* (2008), *A. fernandesi* has a broader distribution than the one we observed, from west to east of Porto Novo. Still, it was not mentioned to occur in Ponta do Sol. Hence, our observation may constitute a new locality for the species. Unfortunately, we did not find any living individuals of that species. Probably more research time is needed to find a living individual. On the island of Santa Luzia, only six endemic species were recorded, namely *A. curralensis*, *A. decoratus*, *A. grahami*, *A. santaluziensis*, *A. saragasae*, *A. navarroi* (Tenorio *et al.* 2017), but we only found and collected a shell of a specimen of *A. curralensis* (Table 1). It is challenging to find cone species on Santa Luzia, probably because of the sea turmoil.

The North-Western Islands, Santo Antão (7.5 million years, My), São Vicente (6.6 My), and Santa Luzia (7 My) are characterized by less endemic cone species and population densities than older islands, such as Sal (25.6 My), Boavista (16.6 My), and Maio (21.1 My) (Afonso & Tenorio 2011, Cunha *et al.* 2005, Cunha *et al.* 2017, Duda & Rolán 2005, Ancochea *et al.* 2015). The initial colonization and radiation of cone snails happened long after the islands were formed, so greater diversity of endemic species on older islands of the archipelago may be due to the higher prevalence of barriers to gene flow and habitats complexity related to changes in island coastlines during repeated periods of low sea levels during glacial maxima (Duda & Rolán 2005, Cunha *et al.* 2017). Therefore, access to an endemic cone population could be more challenging in the north-western islands since their coastline is less flat than on the oldest islands. In addition, the difficulty in finding some species may be associated with their reduced occupation area or small population sizes. Also, the fact that cone snail species are considered night hunters could explain why they are less conspicuous during the afternoon, when sampling was performed.

The morphological character state ‘small' is associated with species with an average individual size between 10–29 mm (Cunha *et al.* 2005, 2008). The most common species on Sal, Boavista, and Maio islands, such as *Conus (Kalloconus) venulatus* and *Conus (Kalloconus) pseudonivifer* (Cunha *et al.* 2008) are large-shelled species and were found in the sand under coral rocks in shallow bays. The habitats appear to be remarkably similar (Rolán 2005) regardless of the size of the shells of the species that inhabit it. In contrast, in the North-Western Cabo Verde Islands, we identified, for the first time, four different types of habitat. In Cabo Verde, few species were found in each habitat type; thus, we have described four types of cone snail habitats. However, the islands with the highest density of individuals have type I and II habitats as the commonest ones. According to Kohn & Nybakken (1975), habitat types are not directly related to prey type. Nevertheless, the relationship between Cabo Verde cone snail species and worm prey species has not yet been considered, increasing even more the difficulty to detect cone snails. It should be noted that supposedly cone snails seek to live in bays protected from large wave movements and where they are protected regardless of the tides (Cunha *et al.* 2005). Surprisingly, in this work, we found cone snail species in the habitat type IV, associated with constant wave breaking, such as *A. freitasi* and *A. denizi*. These species found at habitat IV have shorter shell length, suggesting that this kind of habitat does not provide refuges for larger animals from wave action at high tide (Kohn & Nybakken 1975). These physical difficulties are not encountered in subtidal habitats.

Cone snail diversity could be attributed to the multiplicity of habitats (Kohn 2001). However, the co-occurring species of cone snails in the same habitat (e.g., *Africonus fernandesi*) is due to use of different micro-habitats or probably to a greater extent of different prey species (Khon *et al.* 1975). Thus, to better understand the influence of habitat on the diversity and abundance of cone species, it is essential to develop in-depth studies at micro-habitat level and their correlation with prey types.

CONCLUDING REMARKS

Here, we identified for the first time four types of habitats for Cabo Verde cone snails, suggesting that, in the North-Western Islands of Cabo Verde, the cone snail species spread for more diverse habitats and that is probably is not related directly to their prey. We hypothesized that the evolution of behavioural, morphological, and venom biochemistry traits is the key to adaptation to different habitats. Our results also suggest that the small-shelled cone snail species can habit places with greater hydrodynamics than previously though. However, it is essential to analyse the complex ecological links and interactions in diverse coral reef and non-coral reef habitats to fully understand these new results and more data to test our hypothesis.

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