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DNA sequences disclose a new species of *Africonus* cone snail from São Vicente (Gastropoda: Conidae)

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RESUMO

A sequenciação de genomas mitocondriais completos de espécies de búzios do (sub)género *Africonus*, endémicos de Cabo Verde, permitiu reconstruir as relações filogenéticas entre estas e delimitar e validar o estatuto taxonómico das mesmas. Embora hoje se saiba que muitas espécies descritas são na verdade sinonímias, existem ainda algumas que apresentam divergências nas sequências de ADN suficientemente robustas para merecerem o estatuto de espécie. Este é o caso de algumas populações encontradas na ilha de São Vicente que aqui é descrita como uma nova espécie. A nova espécie assemelha-se na morfologia da concha a *Africonus miruchae* (Röckel, Rolán & Monteiro, 1980), espécie endémica da ilha do Sal, e no seu relacionamento filogenético com *Africonus denizi* Afonso & Tenorio, 2011, endémica de São Vicente. As três espécies apresentam ainda diferenças significativas na morfologia radular.

Palavras-chave: molusco, genoma mitocondrial, endemismo

ABSTRACT

The sequencing of complete mitochondrial genomes of cone species belonging to the (sub)genus *Africonus*, which is endemic to Cabo Verde, has allowed the reconstruction of phylogenetic relationships among these species, as well as delimitation and validation of their taxonomic status. While several species were found to be synonyms, some populations had enough DNA sequence divergence to merit the species status. This is the case of some populations inhabiting São Vicente, which are hereby described as a new species. The new species shares similarity in shell morphology to *Africonus miruchae* (Röckel, Rolán & Monteiro, 1980), endemic to Sal, due to convergence, and with *Africonus denizi* Afonso & Tenorio, 2011, endemic to São Vicente, due to close phylogenetic relationship. Additionally, the three species have significant differences in radular morphology.

Keywords: mollusc, mitochondrial genome, endemism

INTRODUCTION

The Cabo Verde Archipelago is renowned for the high number of endemic cone snail species (Rolán 1990, Monteiro *et al.* 2004, Cunha *et al.* 2005, Duda & Rolán 2005, Peters *et al.* 2016). Distributed in only 4000 km², the 92 endemic cone snail species represent 9% of the species diversity of the group (Tucker & Tenorio 2013). However, many of the Cabo Verdean cone snail populations require a strict delimitation of their specific status (Abalde *et al.* 2017). Taxonomic identification of cone snails has relied mostly on morphological characters of the shell, such as shape, colour and banding patterns. Yet, these traits are prone to homoplasy leading to under- and overestimations of the real number of species when convergence and local population variability, respectively, are not taken into account (Abalde *et al.* 2017).

Since 2013, we have been conducting a systematic sampling of cone snail populations across the archipelago, gathering material for further comparative studies. The ultimate goal is to reconstruct a statistically robust

phylogenetic framework and to integrate it with morphological, ecological, life history, and biogeographical data in order to unravel the evolutionary processes that originated the astonishing diversity of cone snails in this region. First, a robust phylogeny including most of the currently accepted species was recently reconstructed and their taxonomy revised (Abalde *et al.* 2017). DNA sequence divergences below or above a given threshold allowed us postulating synonyms or confirming valid species, respectively (Abalde *et al.* 2017). Additionally, some populations, with sequence divergences above the threshold, were proposed as candidate species. Here, we describe a new species based on two populations previously reported from São Vicente Island (Röckel *et al.* 1980, Rolán 2005), which are morphologically close to *Africonus miruchae* (Röckel, Rolán & Monteiro, 1980) from Sal Island and phylogenetically to *Africonus denizi* Afonso & Tenorio, 2011 from São Vicente.

MATERIAL AND METHODS

Taxonomy follows Tucker & Tenorio (2009, 2013). A map of the localities of the studied specimens was generated using GeoMapApp (<http://www.geomapapp.org>) (Fig.1). We describe shell morphology using the terminology by Röckel *et al.* (1995). Adult shells were measured by MJT with digital callipers. The following metric variables were

used to describe shell morphometry: SL, maximum shell length; MD, maximum diameter; AH, aperture height; MDH, height of maximum diameter; SH, spire height; RD, relative diameter (MD/AH); MDP, relative position of the maximum diameter (MDH/AH); RSH, relative spire height (SH/SL).

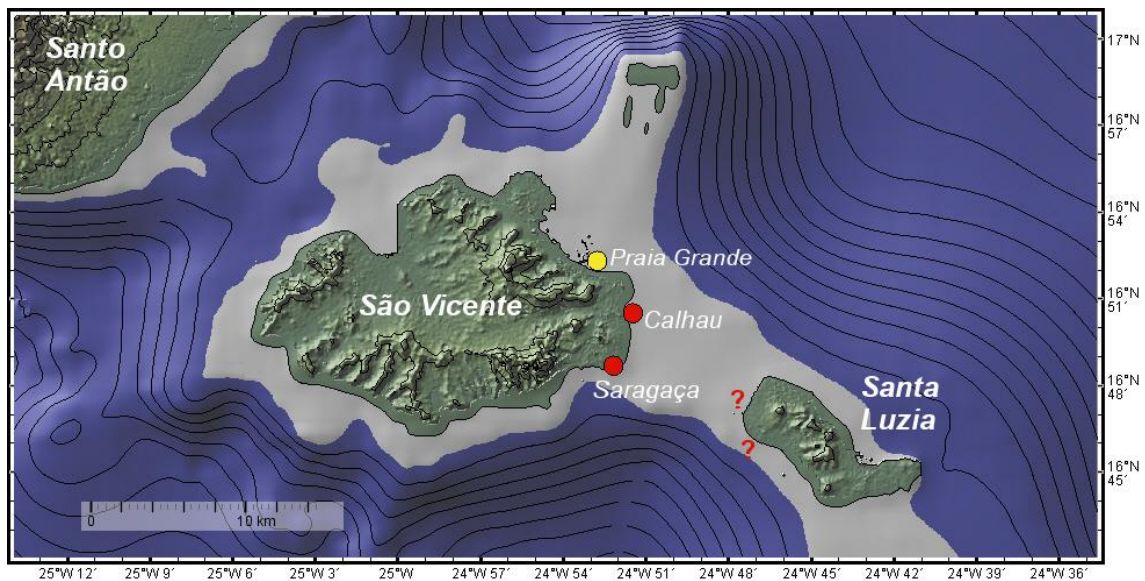


Fig. 1. Map of the localities of the examined specimens of *Africonus* on São Vicente Island. Red dots indicate the locations where specimens of the new species were collected (check Table 1 for further details) and red question marks where the species may also occur. Yellow dots indicate the type locality of *Africonus denizi*. The bathymetric levels are represented by curved lines. Grey areas indicate depths of less than 50 m.

We describe radular morphology using the terminology of Tucker & Tenorio (2009), and variables described in Kohn *et al.* (1999). Shells containing the dried animal inside were digested in concentrated aqueous KOH for 24h. Released radulas were mounted on a slide using Aquatex (Merck) Mounting Medium, and examined under a microscope. The following metric variables, measured by MJT and ER, were used to describe radular morphometry: SL/TL, shell length/radular tooth length; TL/APL, radular tooth size/anterior portion length; 100BL/APL, 100x blade length/anterior portion length. Specimens were deposited in several,

museums and private collections: MNCN Museo Nacional de Ciencias Naturales, Madrid, Spain; MHNS, Museo de Historia Natural de la Universidad de Santiago de Compostela, Spain; MNHN, Muséum National d'Histoire Naturelle, Paris, France; UCV, reference collection of the University of Cabo Verde; MJT, Manuel J. Tenorio's reference collection, Jerez, Spain. A list of all individuals included in the morphological analyses with their taxonomic identifications, specimen codes, repository institution, voucher references, dimensions, and geographical location data is presented (Table 1).

Table 1. Listing of individuals included in the morphological analyses with their taxonomic identifications, voucher code (with the repository institution and specimen codes), shell dimensions (SL, maximum shell length; MD, maximum diameter), and geographical locations (check Fig. 1).

Species	Type/ Code	Voucher code		SL x MD (mm)	Locality
		Institution	Specimen		
<i>A. freitasi</i> sp. nov.	holotype	MNCN	15.05/200008	13.7 x 7.3	Baía do Calhau, São Vicente
	paratype 1	MNCN	15.05/78562	15.9 x 9.6	same data as the holotype
	paratype 2	MNCN	15.05/200010	15.5 x 9.2	same data as the holotype
	paratype 3	MNCN	15.05/78563	13.4 x 8.2	same data as the holotype
	paratype 4	MNCN	15.05/200012	12.9 x 7.3	Baía de Saragaça, São Vicente
	paratype 5	MNCN	15.05/200013	12.4 x 7.2	same data as the paratype 4
	paratype 6	MNCN	15.05/200014	12.4 x 7.1	same data as the paratype 4
	paratype 7	MHNS	100632	12.5 x 7.1	same data as the paratype 4
	paratype 8	MHNS	100633	10.8 x 5.6	same data as the paratype 4
	paratype 9	MNHN	IM-2014-6870	11.3 x 6.3	same data as the paratype 4
	paratype 10	MNHN	IM-2014-6870	12.3 x 7.2	same data as the paratype 4
	paratype 11	UCV	2017/00002	11.6 x 6.2	same data as the paratype 4
paratype 12	UCV	2017/00003	10.8 x 5.6	same data as the holotype	
<i>A. denizi</i>	Holotype	MNCN	15.05/60000	11.6 x 6.3	Praia Grande, São Vicente
<i>A. miruchae</i>		MJT	–	12.9 x 7.2	Terrinha Fina, North of Sal Island

Nucleotide sequences of 13 mitochondrial protein-coding and two rRNA genes from Abalde *et al.* (2017) were aligned using Translator X (Abascal *et al.* 2010) and MAFFT v7 (Kato & Standley 2013), respectively. Uncorrected *p* distances were estimated using MEGA (Kumar *et al.* 2016). Phylogenetic relationships were inferred using maximum likelihood (ML) and Bayesian inference (BI). For ML, we used RAxML

v8.1.16 (Stamatakis 2006) with the rapid hill-climbing algorithm and 10,000 bootstrap pseudoreplicates (BP). For BI, we used MrBayes v3.1.2 (Ronquist & Huelsenbeck 2003), running 10 million generations, sampling every 1000 generations, and discarding the first 25% generations as burn-in. Best partition schemes and best-fit substitution models were identified using PartitionFinder2 (Lanfear *et al.* 2017).

RESULTS

The results of the morphological and molecular analyses are presented in Table 2 and Fig. 2, respectively. Individuals from Calhau and Saragaça populations are described as a new species from São Vicente

given their distinctiveness in several morphological traits (shell size, shell pattern and radular features), and their mitochondrial genome sequence divergences (Fig. 2).

Table 2. Shell morphology variables (SL, maximum shell length; MD, maximum diameter; AH, aperture height; MDH, MD height; SH, spire height) and shell morphometric ratios (RD, relative diameter; MDP, relative MD position; RSH, relative SH), used to compare *A. freitasi* sp. nov., *A. denizi* and *A. miruchae*. The minimum, maximum and average values of each variable for each species are also given.

Species	Shell morphology (mm)					Shell ratios		
	SL	MD	AH	MDH	SH	RD	MDP	RSH
<i>A. freitasi</i> sp. nov.	13.7	7.3	11.0	8.7	2.7	0.66	0.79	0.19
	15.9	9.6	13.7	10.4	2.2	0.70	0.75	0.14
	15.5	9.2	13.1	10.3	2.4	0.70	0.79	0.15
	13.4	8.2	11.5	8.7	1.9	0.71	0.76	0.14
	12.9	7.3	10.8	8.3	2.1	0.67	0.76	0.16
	12.4	7.2	10.7	8.3	1.7	0.68	0.78	0.14
	12.4	7.1	10.3	7.7	2.1	0.69	0.75	0.17
	12.5	7.1	10.9	8.6	1.6	0.65	0.79	0.13
	10.8	5.6	9.4	7.3	1.4	0.60	0.78	0.13
	11.3	6.3	9.4	6.9	1.9	0.67	0.74	0.17
	12.3	7.2	10.5	8.4	1.8	0.69	0.80	0.15
	11.6	6.2	9.2	7.0	2.4	0.67	0.76	0.20
	10.8	5.6	8.8	6.9	2.0	0.64	0.79	0.19
	Minimum	10.8	5.6	8.8	6.9	1.4	0.60	0.74
Maximum	15.9	9.6	13.7	10.4	2.7	0.71	0.80	0.20
Average	12.7	7.2	10.7	8.3	2.0	0.67	0.77	0.16
<i>A. denizi</i>	13.3	7.5	11.2	9.0	2.1	0.67	0.81	0.16
	13.3	7.3	11.0	8.6	2.3	0.66	0.78	0.17
	13.8	7.5	11.2	8.8	2.6	0.67	0.78	0.19
	12.4	6.9	10.5	8.2	1.9	0.66	0.78	0.15
	11.8	6.5	9.7	7.7	2.1	0.67	0.80	0.18
	10.7	5.9	8.8	7.0	1.9	0.67	0.79	0.18
	11.8	6.6	10.0	8.0	1.8	0.66	0.80	0.15
	11.6	6.3	9.7	7.7	1.9	0.65	0.79	0.16
	9.9	5.6	8.2	6.4	1.7	0.68	0.78	0.17
	9.5	5.3	7.9	6.1	1.6	0.67	0.78	0.17
	11.0	6.0	8.8	6.9	2.2	0.69	0.78	0.20
	13.0	7.2	10.6	8.4	2.4	0.68	0.79	0.19
	11.4	6.5	9.5	7.8	1.9	0.68	0.81	0.16
	10.7	5.9	8.6	6.9	2.2	0.69	0.81	0.20
Minimum	9.5	5.3	7.9	6.1	1.6	0.65	0.78	0.15
Maximum	13.8	7.5	11.2	9.0	2.6	0.69	0.81	0.20
Average	11.7	6.5	9.7	7.7	2.0	0.67	0.79	0.17
<i>A. miruchae</i>	10.7	6.3	8.8	6.7	1.8	0.72	0.77	0.17
	13.1	7.5	10.6	8.9	2.4	0.71	0.84	0.19
	12.0	6.8	9.2	7.2	2.8	0.74	0.79	0.23
	12.4	7.5	10.0	7.7	2.3	0.74	0.76	0.19
	11.6	7.1	9.1	7.4	2.5	0.78	0.81	0.22
	14.7	8.1	11.7	9.2	3.0	0.69	0.79	0.20
	11.4	7.1	9.2	7.3	2.1	0.77	0.79	0.19
	12.6	7.2	10.6	8.4	2.0	0.68	0.80	0.16
	12.6	7.0	10.1	8.2	2.4	0.69	0.81	0.20
	13.0	7.6	10.1	8.3	2.8	0.75	0.82	0.22
	12.7	7.2	9.9	8.0	2.8	0.73	0.81	0.22
	11.1	6.4	8.6	6.6	2.5	0.75	0.76	0.22
	11.8	7.3	9.6	7.4	2.2	0.76	0.78	0.19
	11.3	6.7	8.7	7.5	2.6	0.76	0.86	0.23
11.4	6.6	9.3	7.5	2.1	0.71	0.81	0.18	
Minimum	10.7	6.3	8.6	6.6	1.8	0.68	0.76	0.16
Maximum	14.7	8.1	11.7	9.2	3.0	0.78	0.86	0.23
Average	12.1	7.1	9.7	7.8	2.4	0.73	0.80	0.20

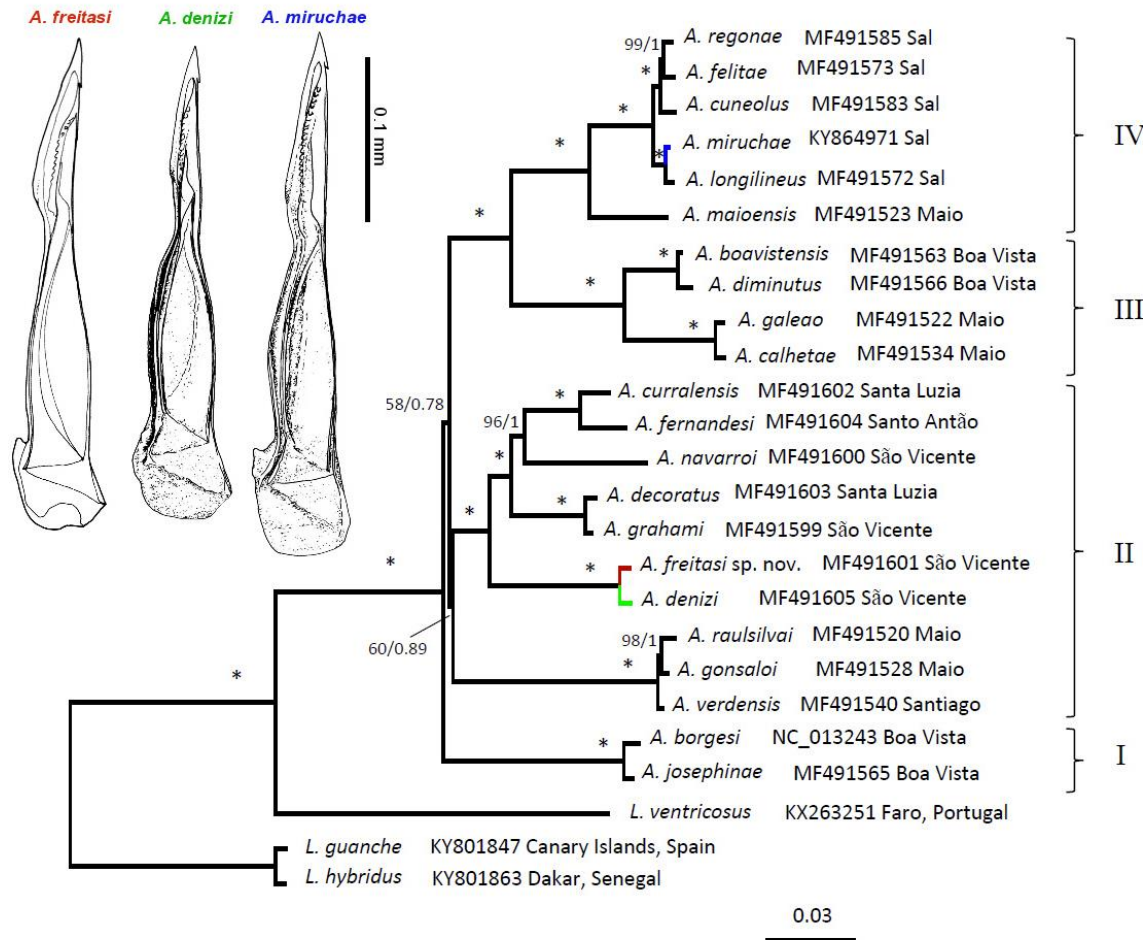


Fig. 2. Phylogeny of *Africonus* from Cabo Verde based on nearly-complete mitochondrial genomes (concatenated protein coding plus rRNA genes analysed at the nucleotide level). Numbers at nodes are statistical support values for ML (bootstrap proportions)/ BI (Bayesian posterior probabilities). An asterisk indicates maximal ML and BI statistical support. Scale bar indicates substitutions/site. Four major lineages (I–IV) were recovered. GenBank accession numbers of the mitochondrial genomes and island distribution are indicated. Cone snails from Senegal and Canary Islands were used as outgroups. The radular teeth of *Africonus freitasi* sp. nov., *A. denizi*, and *A. miruchae* are also represented, all at the same scale.

Africonus freitasi sp. nov.

(Table 1 and 2, Figs. 1–3)

Conus miruchae Röckel *et al.*, 1980: p. 91 (not *Conus miruchae* Röckel *et al.*, 1980);

Conus sp. Rolán, 2005: plate 50

Type material: holotype and 12 paratypes. The holotype is deposited at MNCN under the number 15.05/200008 (Table 1), and Zoobank registration number: urn:lsid:zoobank.org:act:A322AA12-A3FA-45E7-91BD-1DD8E61E4C12.

Material examined: a total of 52 specimens,

collected on São Vicente Island during several expeditions.

Type locality: Calhau, São Vicente Island, Cabo Verde (16°51.116'N, 24°51.983'W).

Distribution and habitat: the species was found on São Vicente Island, Cabo Verde, in Calhau and Saragaça (Fig. 1). Specimens were collected during low tide or by snorkel in shallow water (0.5–1m), often found in crevices of black volcanic rocks. The report of specimens on Santa Luzia Island (Curral and Água Doce) requires confirmation (Fig. 1).

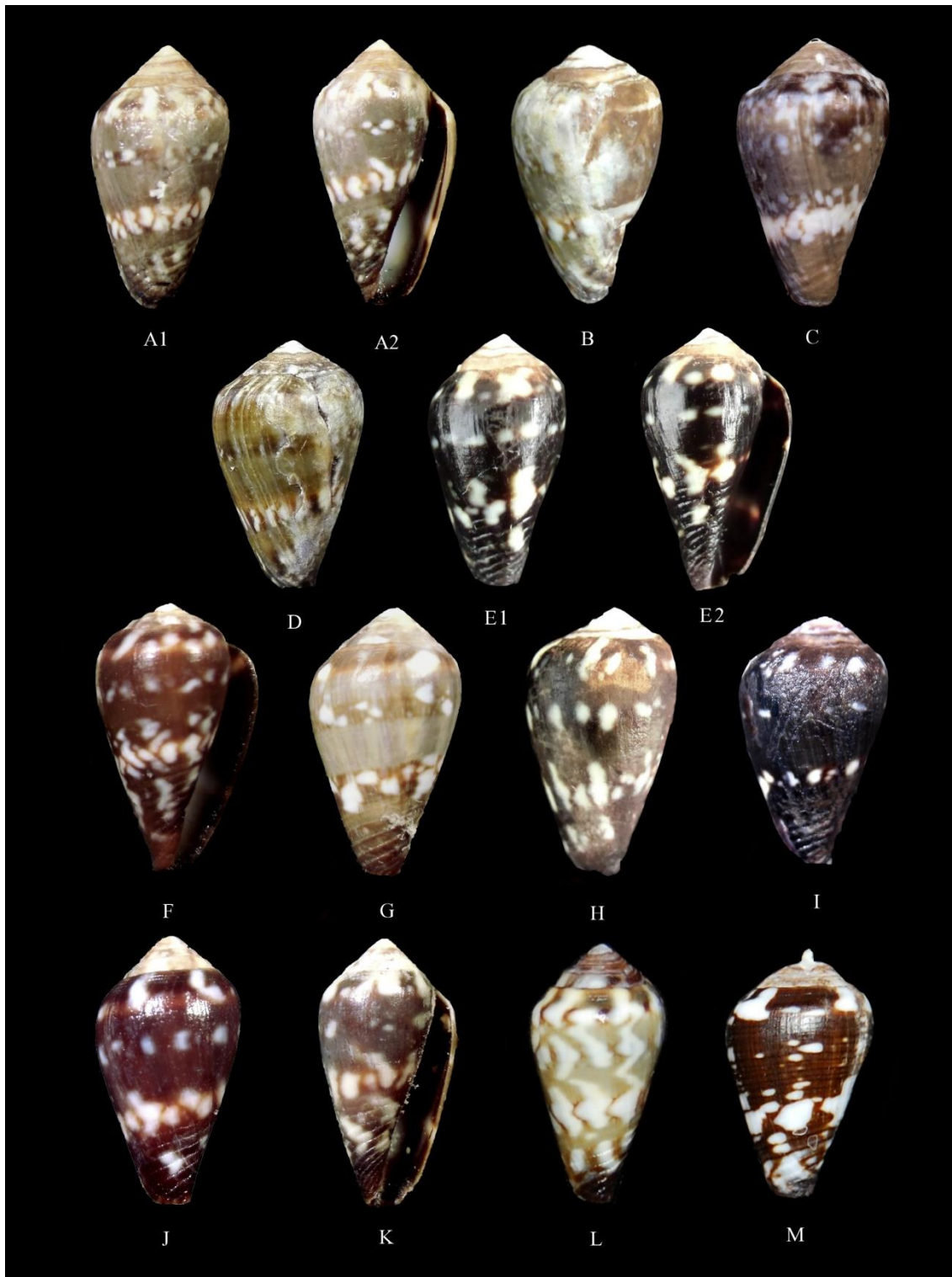


Fig. 3. A–K) *Africonus freitasi* sp. nov.; A1–2) lateral and operculum sides of holotype; B) paratype 1; C) paratype 2; D) paratype 3; E1–2) lateral and operculum sides of paratype 4; F) paratype 5; G) paratype 6; H) paratype 7; I) paratype 8; J) paratype 9; K) operculum side of paratype 12; L) *Africonus denizi*, holotype; M) *Africonus miruchae*. Check Table 1 for further details.

Etymology: the species is named after Rui Freitas, marine biologist and professor at Faculdade de Engenharia e Ciências do Mar, University of Cabo Verde. Rui has conducted extensive research on the littoral ichthyofauna of Cabo Verde Islands and has provided over the years great support to our sampling, which ultimately led to the discovery of the new species.

Diagnosis: *Africonus* characterized by the following combination of morphological characters: shell very small; ventricosely conical to broadly ovate; spire black with white blotches; last whorl black, dark brown or dark olive green with white blotches in spiral bands; radular tooth with 10–15 denticles in the serration not reaching the apical portion; small base with a spur. Additionally, phylogenetic analyses clearly indicate that *A. freitasi* and *A. denizi* are genetically well-differentiated sister taxa with a genetic *p*-distance of 0.4% in the mitochondrial genome.

Description of the shell: morphometric data are presented in Table 2. Shell always very worn and eroded, even for live specimens. Shell very small, broadly and ventricosely conical to broadly ovate in profile. Spire moderate, most often eroded, of straight profile. Teleoconch whorls flat or slightly convex with fine cords. Shoulder rounded. Last whorl sides straight or slightly convex. Spire black with white blotches. Body whorl smooth except for 6–10 spiral grooves present on the basal third of the body whorl. Ground colour of the last whorl black, dark brown or dark olive green. Pattern consisting of white blotches arranged in spiral bands distributed on the shoulder and spire, around the mid-body, and near the base. There is a narrower band of white blotches present below the shoulder. Inside of the outer lip dark brown with two lighter bands. Colour becoming lighter towards the interior of the aperture, which is bluish white deep within. Shells examined very homogeneous in size and pattern, but variable in ground colour (Fig. 3).

Periostracum very thin, yellow and translucent. Operculum small.

Living animal and radula: adult animal completely black. Radula studied from five specimens, including paratype 2 (Fig. 2). Between 40–55 teeth in radular sac. Radular tooth of medium relative size ($SL/TL = 40\text{--}44$), narrow and slender, with an almost indistinct apical barb. Anterior section shorter than the posterior section of the tooth ($TL/APL = 2.4\text{--}2.6$). Waist evident but not very pronounced. Blade rounded and not very pronounced, covering most of the anterior section ($100BL/APL = 75\text{--}83\%$). Serration with 10–15 denticles, which do not reach the apical portion, arranged in one row ending in a small terminating cusp. Base small, with a spur.

Differential diagnosis: *A. freitasi* sp. nov. (Fig. 3A–K) is similar to *A. denizi* (Fig. 3L) and *A. miruchae* (Fig. 3M) in shell morphology, and in fact it has been confused with these taxa in the past (Röckel *et al.* 1980; Peters *et al.* 2016). However, some subtle differences are observed. *A. denizi* has a predominantly white spire with alternating dark brown axial blotches instead of black with white blotches. Last whorl in *A. denizi* is olive-green to light olive-green, normally patterned with three interrupted spiral bands formed by white blotches tinged with brown to dark brown markings. In *A. freitasi* sp. nov., the ground colour is black or very dark olive green, although the pattern of white blotches might occasionally resemble that of *A. denizi*. The animal in *A. denizi* is dark reddish-grey, but black in the case of *A. freitasi* sp. nov. The two species seem to be allopatric in distribution: *A. denizi* has only been found in São Vicente at Praia Grande, a large, sandy bay north of Calhau, where *A. freitasi* sp. nov. does not occur. The radular teeth of these two species are similar (Fig. 2), but the basal spur is much more prominent and developed in the case of *A. freitasi* sp. nov. The shell of *A. miruchae* is remarkably similar to that of *A. freitasi* sp. nov. The latter

has a more elongated shape (RD 0.60–0.71 versus 0.68–0.78 in *A. miruchae*). These two species also differ in radular characters: *A. miruchae* has more denticles in the serration (15–22) reaching the apical portion of the tooth, whereas *A. freitasi* sp. nov. has only 10 to 15 denticles which do not reach the apical portion (Fig. 2).

Phylogeny: The analysed species of *Africonus* were grouped into four main lineages with high statistical support (Fig. 3). *A. miruchae* was placed within lineage IV with other species from Sal Island. *A. denizi* and *A. freitasi* are sister group species placed within lineage II in a clade that also contains species from Santo Antão, São Vicente, and Santa Luzia.

DISCUSSION

Phylogenetic analyses show that *A. freitasi* sp. nov., *A. denizi*, and *A. miruchae* are distinct species despite their partial similarity in shell morphology. The reconstructed phylogenies placed *A. freitasi* sp. nov. sister to *A. denizi*, whereas *A. miruchae* was recovered in a distant clade (Fig. 2). This result reflects the biogeography of these species as *A. freitasi* sp. nov. and *A. denizi* are both found on São Vicente, whereas *A. miruchae* is endemic to Sal. The uncorrected *p*-distance between *A. freitasi* sp. nov. and *A. denizi* was 0.4%, just above the established threshold for species delimitation and validation in this hyperdiverse group (see Abalde *et al.* 2017). The phenotypic resemblance of the shell of *A. freitasi* sp. nov. and *A. miruchae* is possibly the result of convergence given their separate placement in the reconstructed phylogeny and their disjoint distribution in different islands whereas similarity between *A. freitasi* sp. nov.

and *A. denizi* may reflect their close phylogenetic relationship (sharing a relatively recent last common ancestor). Nonetheless, the results here obtained should be further corroborated with nuclear sequence data. An interesting evolutionary pattern derived from the phylogeny is that Windward Islands at the northwest tip of the Cabo Verde Archipelago have fewer endemic cone species but of older origin (longer branches in the tree) when compared to geologically older islands as Sal, Boavista and Maio, which hold younger radiations. This pattern may reflect the fewer available niches (intertidal and subtidal rocky shores) in Santo Antão, São Vicente, and Santa Luzia. *A. freitasi* sp. nov. is not an uncommon species in its distribution area, although it is easily overlooked due to its small size. Its conservation status should be evaluated.

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