

Review of the *Voluta musica* Complex

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ABSTRACT The distinctive morphology, color pattern, and isolated geographic locations of the various proposed taxa of the *Voluta musica* complex are discussed and specimens of the various taxa are illustrated. Evidence shows that populations of ancestral *V. musica* became genetically isolated on offshore islands during interglacial times, due to the associated higher sea levels during the Neogene, resulting in a species swarm of closely-related allopatric species. The following taxa are recognized as full species, and these include: *Voluta musica*, *V. carneolata*, *V. thiarella*, *V. damula*, and *V. typica*.

KEY WORDS Volutidae, *Voluta musica*, *Voluta damula*, *Voluta typica*, *Voluta carneolata*, *Voluta thiarella*, *Voluta musica* form *guiniaca*, *Voluta musica* form *laevigata*, *Voluta musica plicata*, *Voluta cantaurana*, biogeography, direct developers, barriers to dispersal

INTRODUCTION

Voluta musica Linnaeus, 1758 is a well-known tropical western Atlantic volute which has been reported from the “West Indies”, from the northern coast of South America, east across the coastline of Venezuela, then northwards up the Lesser Antilles Arc (Weaver & DuPont, 1970). Over the last 200 years, a number of related taxa at the subspecific level have been named based upon shell shape, sculpture, color pattern, and geographic localities. These include: *Voluta musica carneolata* Lamarck, 1811, *Voluta musica thiarella* Lamarck, 1811, *Voluta musica laevigata* Lamarck, 1811, *Voluta musica guiniaca* Lamarck, 1811, *Voluta musica damula* Dall, 1907, and *Voluta musica typica* Dall, 1907. In 1907, Dall performed the first extensive review of the *Voluta musica* complex which included examination of numerous specimens in the U.S. National Museum and an extensive literature review. Later in 1965, Olsson reviewed the genus *Voluta*, which included the examination and study of Lamarck’s type

specimens housed in the Geneva Museum in Switzerland. While undertaking this study of the *V. musica* species complex, care was taken to ensure that specimens included herein had accurate and credible locality data.

During the 1940’s and early 1950’s, extensive field work focusing on the *Voluta musica* complex was conducted by Verrill wherein he personally collected and studied nearly 500 specimens. The results were published in a series of articles in the Conchology Club of Southern California Minutes between 1950 and 1954 (Verrill, 1950; Verrill, 1953a; Verrill, 1953b; Verrill, 1954). In those works, Verrill named five new taxa within the *Voluta musica* complex, including *V. musica sanguinea*, *V. musica alba*, *V. musica alfordi*, *V. musica tobagoensis*, and *V. musica margaritana*. Unfortunately, no type specimens were designated or deposited in any institutions. Further, no voucher specimens from Verrill’s studies were located in the Natural History Museum of Los Angeles, the Santa Barbara

Museum of Natural History, or the Florida Museum of Natural History (Personal communications with Lindsey Groves, Henry Chaney, and John Slapcinsky). Consequently, Verrill's taxa are considered *nomina nuda*.

Clench and Turner noted that "*Voluta musica* is an exceedingly variable species in all of its shell morphology", however they did not find or did not consider that these variations may have had geographic significance (Clench & Turner, 1964). Unfortunately, as was typical for the era, Abbott stated in *American Seashells* that "[a] number of useless names have been applied to the numerous variations of this species" (Abbott, 1974). Abbott synonymized all prior published names without any analysis or discussion, utilizing "taxonomy by decree." Admittedly, Abbott should not have included *V. musica* in *American Seashells* due to these taxa being outside the scope of that book. This broad overreach fails to take into account the ecology and embryonic development of these animals, limits to dispersal, biogeographical distribution, varying sea levels over geological time, genetic isolation, and evolution as seen in the fossil record.

Voluta musica is known to have direct development, with an encapsulated veliger stage which is unable to disperse until after metamorphosis into a crawl-away hatchling snail. These tiny volutes measure 6.4 to 8.6 mm, have a small complete shell, and a pigmented foot and siphon (Penchaszadeh & Miloslavich, 2001; Rangel *et al.* 2011). *Voluta musica* was previously described as inhabiting a relatively shallow habitat range in the littoral zone to approximately 5 fathoms, or 9.1 meters in depth (Weaver & DuPont, 1970). Recently, detailed ecological studies have shown that *V. musica* lives in shallow waters on sand and coralline-lime bottoms often associated with "turtle grass" *Thalassia testudinum* K.D. Koenig, 1805,

and prefer to lay their eggs on valves of the Pen Shells *Atrina seminuda* (Lamarck, 1819), *Pinna carnea* Gmelin, 1791, and the Ark Shell *Anadara floridiana* (Conrad, 1869) in shallow water turtle grass beds (von Cosel, 1976; Flores, 1978; Rangel *et al.* 2011). The western distributional limit of *V. musica* is demarcated by a dramatic change in substrate from its preferred habitat of sand and coralline-lime bottoms to muddy, organic-rich reducing environments from the effluent of the Atrato, Sinu, and Magdalena rivers (Petuch, 2013). This habitat is preferred by *Voluta virescens* Lightfoot, 1786 and *Voluta lacertina* Petuch, 1990 (Petuch, 2013). Similarly, the eastern distributional limit of *V. musica* ends at the western edge of the Venezuelan Subprovince, and northern edge of the Surinamian Subprovince, which is due to a similar change in substrate, from sand and coralline-lime bottoms with turtle grass beds to with organic-rich muddy bottoms along mangrove-lined shores (Petuch, 2013). This change in environment also creates an ecological barrier which is the result of a tremendous amount of fresh water effluent from hundreds of rivers extending from the Orinoco River Delta near southern Trinidad, south towards Brazil, in which no *Voluta* species are represented (Petuch, 2013).

Over the last million years (middle Pleistocene) sea levels have fluctuated wildly, often dropping more than 300 to 400 meters below present sea level (Murray-Wallace, C.V. Woodroffe, & C.D. Woodroffe, 2014). In more recent geological time, sea levels have risen 125 to 130 meters during the last 75,000 years as a result of the last glacial minimum (Petuch, 1981; Carlson, 2011). Consequently, *V. musica* populations that developed on offshore islands since the late Pleistocene, have become genetically isolated, and have evolved into closely related allopatric species.

Hundreds of specimens with accurate locality data are examined here from along the coast of South America ranging from Santa Marta, Colombia in the west, along the Venezuelan coast to Trinidad, as well as the offshore islands of Aruba, Curaçao and Bonaire, and then northwards up the Lesser Antilles arc from Tobago to Martinique. While there is some anecdotal evidence, no specimens of *V. musica* from the northern islands of Dominica, Barbuda, and St. Kitts, with accurate locality data were available for review in this study. Additionally, there are supposed records of two specimens from Puerto Rico, neither of which have been shown to have accurate collection data (Warmke & Abbott, 1962; personal communication with Scott Robichaud). These specimens labeled as from Puerto Rican are extremely unlikely to have been found as living animals as the Muertos Trough, an 8,376 meters deep and 800 km long oceanic trench, acts as an insurmountable barrier to dispersal for mollusks that are direct developers.

SYSTEMATICS

Class	Gastropoda Cuvier, 1795
Subclass	Caenogastropoda Cox, 1960
Order	Neogastropoda Wenz, 1938
Superfamily	Volutoidea Rafinesque, 1815
Family	Volutidae Rafinesque, 1815
Subfamily	Volutinae Rafinesque, 1815
Genus	<i>Voluta</i> Linnaeus, 1758

SPECIES ACCOUNTS

Voluta musica Linnaeus, 1758
(Figure 1, Plates 1 and 2)

Original Description. “Testa marginata fusiformi, antfractibus spinis obtusis, columella octoplicata, labro laevi crassiusculo.” (L. 1758)

Translation. “shell marginated fusiform, obtuse spines, an eight-fold columella, the left lip is thicker.”

Re-Description. “Shell is variable in color and shape. Typically it is medium in size and is solid, with a moderately extended spire. Protoconch is turbinate and smooth, of about three whorls. Teloconch has four and a half longitudinally plicate whorls, strongly knobbed at the shoulders. Suture is irregular and impressed. Aperture is long and rather wide. The outer lip is reflected; interior peach colored. Siphonal notch is deep; fasciole present. Columella is glazed, with numerous folds, the anterior five or six forming strong plaits. Base color ivory or pinkish-white, overlaid with an intricate design of spiral lines and dots resembling written music. Inner margin of outer lip often has a number of large brown spots.” (Weaver & DuPont, 1970)

Type. Lectotype selected by Olsson 1965, Linnaean Collection, Linnean Society of London, No. 370, measuring 38.0 mm in length.

Type Locality. None given.



Figure 1. Line drawing of a *V. musica* specimen from the type lot as illustrated by Kiener, 1839.

Voluta musica thiarella Lamarck, 1811
(Figure 2, Plate 8)

Original Description. “Ovato-oblonga, alba, subtuberculata; lineus transversis parallelis; fascia punctata; ad margines albo fuscoque articulata.” (Lamarck, 1811)

Translation. “Ovate-oblong, white, subtuberculate; a parallel transverse line; dotted band; articulated at the edges white and brown.”

Modern Re-Description. Although Dall did not re-describe *thiarella* in his monumental work as first reviser (Dall, 1907), Verrill did provide a modern description of the taxa, stating: “distinguished by its pink or pale flesh-colored ground color, red musical staff, absence of color markings on the shoulder nodules, bluish spots above and below these, the rich salmon or orange interior, the numerous columnar plications (fourteen to sixteen), the orange-colored nucleus and the small, widely spaced few spots on the edge of the lip. These are often absent.” (Verrill, 1950)

Type. Lamarck collection in Geneva, measuring 67.2 mm in length.

Type Locality. None given.

Comments. “The type specimen of *V. thiarella* at Geneva agrees well with the figure in the Encyclopédie as to size, shape, and color pattern. Its general color is a pale brown, its markings of a darker shade. The surface is smooth except for obscure spirals on the sutural collar. Columella with ten plaits, the five lower ones strongest. The specimen measures: - length 67.2 mm, diameter 37.5 mm” (Olsson, 1965).



Figure 2. *V. musica thiarella* type specimen as illustrated by Kiener, 1839.

Voluta musica guiniaca Lamarck, 1811
(Figure 3, Plate 1 Figures A, C, & E, Plate 2
Figures G-I)

Original Description. “Ovata, subtuberculata, ablida, violaceo nebulosa; lineus fuscis decussatis; fasciis punctatis; columella plicis quatuordecim.” (Lamarck, 1811)

Translation. “Oval, subtuberculate, pale, misty violet; a line of broken brown; dotted bands; a sieve of fourteen folds.”

Modern Re-Description. Although Dall did not re-describe *guiniaca* in his monumental work as first reviser (Dall, 1907), Verrill noted that this subspecies was found off Isla Margarita, Venezuela, and Grenada, and provided a modern description of the taxa, stating: “Ground color ochreous or pale orange. Aperture dull yellow. 10 to 12 columnar plications. Longitudinal ribs scarcely indicated. Shoulder nodules low, obtuse, rounded. Spire extended, pyramidal. Large heavy dark-brown blotches and smaller dots scattered over the entire shell,

often joining to completely conceal the “staff” lines. Many small deep orange spots on edge of lip, not raised. Some specimens have a pinkish cast but the numerous heavy brown blotches are very distinctive.” (Verrill, 1950)

Type. Lamarck collection in Geneva, measuring 61.5 mm in length.

Type Locality. None given.



Figure 3. *V. musica guiniaca* type specimen as illustrated by Kiener, 1839.

Voluta musica laevigata Lamarck, 1811
(Figure 4, Plate 2 Figures A-F)

Original Description. “Ovata, muticá, obsoleté nodulosa, albida, cinereo-violascens; fasciá lineis fuscis, subdecussatis pictá; columellá octo-plicatá.” (Lamarck, 1811)

Translation. “Ovate, muted, obsolete nodular, whitish, greyish-violet; the sash was painted with brown lines, undercut; eight-folded columella.”

Re-Description (from Dall, 1907). “Shell oval, with seven to nine low, hardly nodulous, ribs;

nucleus brown; yellowish with crowded dark zigzag blotches, the parallel brown lines tending to become obsolete; spiral sculpture faint or absent in front of the suture and normal near the canal; aperture yellowish-pink; outer lip with brown spots which sometimes project as nodules, the pillar lip with eight to thirteen plaits.”

Type: Lamarck collection in Geneva.

Type Locality. None given.

Other Specimens. U.S. National Museum Nos. 75268, 122218.

Locality. La Guaira, Venezuela; Gulf of Venezuela (E.J. Petuch, personal communication)

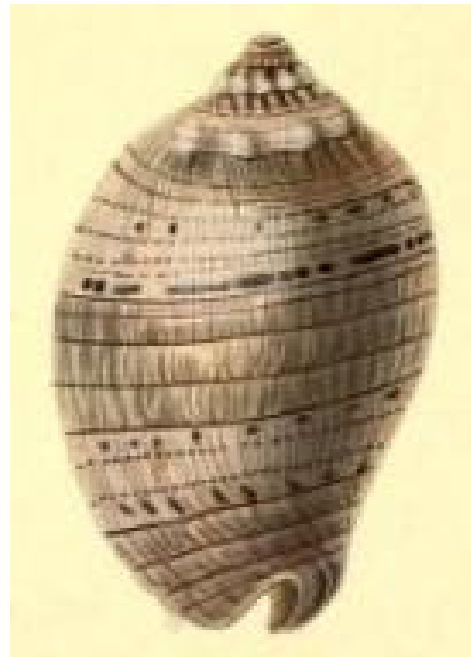


Figure 4. *V. musica laevigata* type specimen as illustrated by Kiener, 1839.

Voluta musica carneolata Lamarck, 1811
(Figure 5, Plate 7)

Original Description. “Ovata, muticá, albido lutea vel crocea; lineis punctis masculinesque fasciatis; costis longitudinalibus obtusis.” (Lamarck, 1811)

Translation. “Ovate, muted, whitish-yellow or crimson; lined with dotted lines and masculine; obtuse longitudinal ribs

Re-Description (from Dall, 1907). “Shell oval, with prevalent red tracery over a flesh-colored ground, smaller than the variety *thairella* Lamarck, and narrower than the typical *musica*; nucleus orange-yellow; with eight to eleven low ribs, feebly nodose at the shoulder; middle of the whorl smooth, but with spiral cords or flat ridges in front of the suture or near the canal; aperture orange-pink with brown spots on the outer lip and nine to eleven plaits on the pillar lip.”



Figure 5. *V. musica carneolata* type specimen as illustrated by Kiener, 1839.

Type. Lamarck collection in Geneva, measuring 49.0 mm in length.

Type Locality. None given.

Other Specimens. U.S. National Museum Nos. 2937, 54516, 54520, 118050, 123452, and 129246.

Locality. Barbados.

Comments. “*V. carneolata* is a valid species distinguished easily from *V. musica* by its sculpture of strong, spiral cords, shape, and color design.” (Olsson 1965) “The type specimen at Geneva shows strong spiral cords in the sutural zone and around the base. The color is a delicate, creamy rose, the markings in a rich brown. The inner lip has 10 plaits, heaviest below, weakening above. The protoconch is large like that of *V. musica*. Length 49 mm, diameter 38.2 mm. Type.” (Olsson 1965)

Voluta musica plicata Dillwyn, 1817
(Figure 6, cf. Plate 9)

Description. “Shell emarginate, longitudinally plaited and angular, and transversely grooved; spire nodulous; pillar with twelve plaits, and the throat orange.” (Dillwyn, 1817)

Modern Re-Description.

This taxa was not mentioned or treated by Dall, however Verrill noted that this subspecies was the common form found at Isla Margarita, Venezuela, Grenada, Carriacou, and Bequa (but not found north of the Grenadines), and provided a modern description of the taxa, stating: “Ground color very pale buff to almost white. Musical staff, small scattered blotches and numerous fine specks fawn color or pale orange-brown. Nucleus straw-color. Interior pale yellowish-white. Markings on edge of lip deep brown, arranged in pairs evenly spaced, slightly raised above surface. Columnar plications eleven.” (Verrill, 1950)

Type Locality. None given.

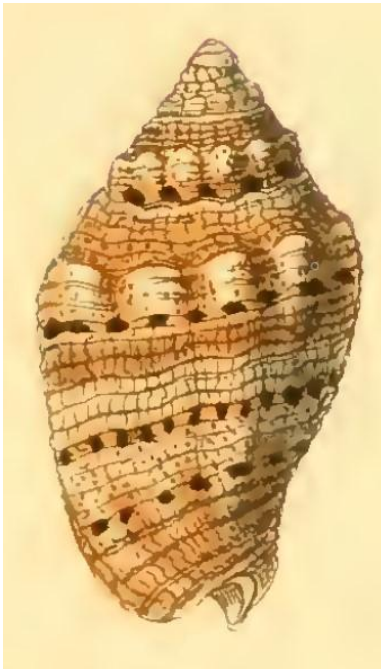


Figure 6. *V. musica plicata* type specimen as illustrated in G.B. Sowerby, II 1847.

Voluta musica typica Dall, 1907
(Figure 7, Plate 5)

Description. “Shell short, wide, buff, or yellowish white under usual brownish tracery, with six or seven subspinose stout ribs at the shoulder of the whorl; nucleus dark brown; sparse spiral sculpture near the canal only; interior of the aperture usually white; outer lip with black spots, pillar lip with nine to eleven plaits.” (Dall, 1907)

Type Specimens. U.S. National Museum Nos. 54517 holotype, 54522 paratype. Neither specimen is illustrated on the USNM website.

Type Locality. Tobago.

Comments. *V. musica typica* has distinctive broad shoulders, proportionately large shoulder knobs, and one of the narrowest, most elevated, proportionately smallest and most projecting protoconch of all the taxa in the complex. Protoconch morphology is an important character in the genus *Voluta* (Petuch, 1981).



Figure 7. *V. musica typica* specimen from the Berschauer Collection, photographed by the author.

Voluta musica damula Dall, 1907
(Figure 8, Plate 4 Figures A-D)

Description. “Shell small, oval, with eight or nine low ribs, slightly nodulous at the shoulder; nucleus pale brown; ground color whitish, with the usual tracery in fawn-color and pale brown, with vertical brown fringe-like lines and distinct spiral sculpture in front of the suture and four or five flattish ridges on the canal; aperture livid pink, or sometimes violaceous, with brown spots on the outer lip and nine or ten plaits on the inner lip; a specimen of four whorls, beside the nucleus, measures 42 mm. long and 21 mm. wide.” (Dall, 1907)

Type Specimens. U.S. National Museum Nos. 54521 holotype, and 29249 paratype.

Type Locality. Curaçao.



Figure 8. *V. musica damula* type specimen from the USNM.

DISCUSSION

Bathymetric maps with depths denoted in various shades of blue were accessed via the National Oceanic and Atmospheric Administration (“NOAA”) (NOAA, 2023). A black line has been drawn on a NOAA bathymetric map of the southern Caribbean and northern coastline of South America along the present day 100 meter contour to reflect the approximate coast line during the period of greatest land emergence during the late Pleistocene (Figure 9). This shows where the coast line would have been during that time period. The presumed distribution of the ancestral population of *Voluta musica* would have been found at depths of 15 to 20 meters from these ancient coastlines.



Figure 9. Bathymetric map with 100 m contour, reflecting coast line during greatest emergence (Adapted from NOAA, 2023).

The localities where modern-day populations of the *Voluta musica* complex have the greatest morphological variability is presumably where the species complex originated before spreading out to inhabit other areas. The *V. musica* complex is currently known to range from Ensenada de Chengae, Santa Marta, Colombia (von Cosel, 1976) eastward along the Venezuelan coast to just past Trinidad, and then northwards along the Lesser Antilles chain of islands (Dall, 1907; Verrill, 1950). The soft bottom substrates east of Ensenada de Chengae, Santa Marta, Colombia, consist of a muddy mineral sand which forms the eastern barrier for *V. musica*, and is the preferred habitat of *Voluta virescens* Lightfoot, 1786 (von Cosel, 1976). The map in Figure 9 illustrates the 100 meter contour line where the late Pleistocene coast line would have been approximately 75,000 years ago. The ancestral population of *V. musica* would have inhabited the shallow waters along the north coast of modern day Santa Marta, Colombia across Venezuela, and a long peninsula reaching northward into the Caribbean up to and including what is now the island of Martinique. The lower sea levels during the late Pleistocene would have exposed a majority of this area as a peninsula, thereby providing easy dispersal along that coast. However, dispersal beyond the northern tip of this ancient peninsula (an area that is now the island of Martinique) to Dominica and the northern islands would likely have been impossible due to deep oceanic trenches and the low dispersal ability of these volutid taxa.

In 1973 Gibson-Smith examined and studied approximately 250 recent specimens of *Voluta musica* (from the Venezuelan Subprovince in the Holocene) as well as over 40 fossil Miocene and Pliocene age *Voluta* specimens from what was then the Puntagavilian Subprovince of the Gatunian Province (Gibson-Smith, 1973; Petuch, 2004). As a result of this study Gibson-Smith

determined that *V. musica* appeared to have evolved in the Pleistocene, and named *Voluta cantaurana* from the early Miocene as the ancestral species to *V. musica* (Gibson-Smith, 1973; Petuch, 1988). During interglacial times and the associated eustatic highs during the Neogene (Petuch, 1981; Carlson, 2011), populations of *V. musica* became geographically isolated on offshore islands both along the coast of South America, and some of the southernmost islands of what are now known as the Lesser Antilles. Those isolated *V. musica* populations have become genetically isolated, and have had the opportunity to evolve into closely related allopatric species over the last million years (Petuch, 1981).

A black line has been drawn on a NOAA bathymetric map of the northern coastline of South America and Lesser Antilles islands along the present day 20 meter contour to reflect the presumed current distribution of the *V. musica* complex, including all islands in this study where *V. musica* with accurate locality data have been found (Figure 10). There are a few anecdotal records of *V. musica* from the northern islands of Dominica, Barbuda, and St. Kitts, unfortunately no specimens with accurate locality data were available for review in this study. The map in Figure 10 reflects the present day coast lines and the 20 meter contour reflects the presumed present day geographical distribution of the *Voluta musica* complex, excluding the anecdotal records from northern islands of the Grenadian Subprovince. There are also anecdotal records of two *V. musica* specimens from Puerto Rico (Warmke & Abbott, 1962; Scott Robichaud, personal communication). However, the Muertos Trench (5,000 to 8,380 m in depth) acts as a barrier to dispersal and makes this exceedingly unlikely for a shallow water volute species.

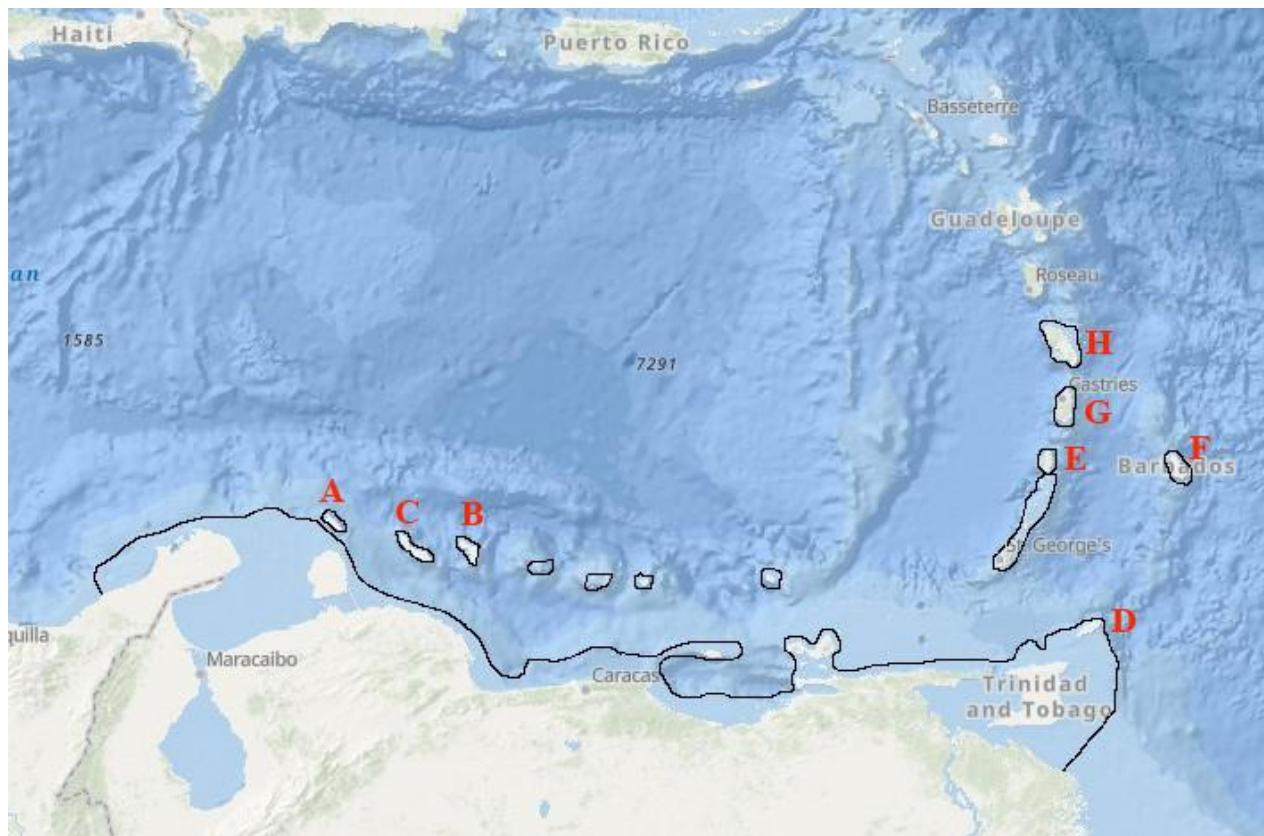


Figure 10. Bathymetric map with 20 m contour, reflecting the known present day geographical distribution of the *Voluta musica* complex (Adapted from NOAA, 2023). Isolated populations are found on the following islands: **A**= Aruba; **B**= Bonaire; **C**= Curaçao; **D**= Tobago; **E**= St. Vincent and the Grenadines; **F**= Barbados; **G**= St. Lucia; **H**= Martinique.

The largest contiguous population of *V. musica* presently is found from Santa Marta, Colombia eastward along the Venezuelan coast to just south of Trinidad (the Venezuelan Subprovince), and as expected individual shells from this population exhibit the greatest variability in morphology, pattern, and color (See Plates 1 and 2). These facts are consistent with Gibson-Smith's hypothesis that *V. musica*'s ancestral population evolved off the coast of Venezuela (Gibson-Smith, 1973).

Bathymetric Barriers to Dispersal:

It is unlikely that there are extant populations of the *V. musica* complex north of Martinique. This is due to the presence of deep oceanic

passages and trenches that separate island groups and prevent dispersal of direct developers (Penchaszadeh & Miloslavich, 2001; Rangel *et al.* 2011). These bathymetric barriers to dispersal would prevent colonization of the *V. musica* complex to the northern islands of the Grenadian Subprovince. Some of the most significant deep oceanic passages and trenches from south to north include:

- The **Martinique Passage** between the islands of Martinique and Dominica is 1,400 m to 2,150 m deep (NOAA, 2023), which is a clear barrier to dispersal.
- The **Dominica Passage** between the islands of Dominica and Guadalupe is 1,250 m to 2,000

m deep (NOAA, 2023), which is a clear barrier to dispersal.

- The **Guadalupe Passage** north of Guadalupe is 1,180 m to 3,000 m deep (NOAA, 2023), which is a clear barrier to dispersal to northern islands of the Lesser Antilles including: Montserrat, St. Kitts & Nevis, St. Thomas, St. Croix, St. John's, Barbuda, St. Barthelemy, St. Maarten, Anguilla, U.S. Virgin Islands, British Virgin Islands, Vieques, Culebra.

- The **Muertos Trough** south of Puerto Rico ranges in depth from 5,000 m to 8,380 m (NOAA, 2023), which is a clear barrier to dispersal.

Accordingly, sound oceanographic, ecological, and biogeographical evidence support the conclusion that living populations of taxa in the *V. musica* complex do not currently exist north of Martinique in the Lesser Antilles island chain.

Known populations in the *Voluta musica* complex:

The largest contiguous population of *Voluta musica* is found in the Venezuelan Subprovince from Ensenada de Chengae, Santa Marta, Colombia eastward along the Venezuelan coast to south of Trinidad. Photos of specimens from this coastal population are illustrated on Plates 1 and 2. As can be seen these specimens exhibit a wide range of morphological and color pattern variability. There does not appear to be any good morphological or biogeographical reason to distinguish between *Voluta musica guiniaca* and *V. musica*, other than the fact that *guiniaca* has slightly smaller shoulder knobs. Images of classic *V. musica* specimens with heavier shoulder knobs are illustrated on Plate 1, and images of specimens with reduced to practically non-existent shoulder knobs, similar to what has been named *V. musica laevigata* Lamarck, 1811,

are illustrated on Plate 2. *V. musica laevigata* has been reportedly found as the exclusive form found in the Gulf of Venezuela along the Paraguaná Penninsula (Petuch, personal communication). *V. musica laevigata* has also been reported from the Paraguaná Penninsula to Puerto la Cruz, Venezuela (Gibson-Smith, 1973), which would make it a sympatric population with classic heavily knobbed forms of *V. musica*. From the specimens reviewed in this study there do not appear to be any intermediate forms between these two morphologies, which is suggestive of either distinct sympatric breeding populations or distinct ecomorphological phenotypes. Accordingly, the Gulf of Venezuela population which most closely resembles the type of *V. musica laevigata* warrants further study. Some *V. musica laevigata* specimens have also been confused with *Voluta musica carneolata* Lamarck, 1811, which it superficially resembles primarily due to the pale orange coloration of some Venezuelan specimens (Gibson-Smith, 1973). However, color alone is not controlling and the morphology of *V. musica carneolata* is distinct, and based upon all verifiable known records *carneolata* is endemic to Barbados.

The closest isolated island populations in the *Voluta musica* complex to the Venezuelan coast would be those found on Aruba, Curaçao and Bonaire. Plate 3 illustrates a number of specimens from Aruba, showing a fairly wide range of variability. These specimens exhibit similar degrees of shape, form, and color pattern to the more heavily knobbed variety found along the Venezuelan coast. These similarities make sense considering that the Aruban population is the farthest east among the various island populations, is located on the continental shelf, and is one of the closest islands to the present day Venezuelan coast. In fact the lectotype of *V. musica* in the Linnaean Collection strongly resembles some of the paler

specimens from Aruba. Accordingly, the Aruban population is designated herein as *V. musica*. Dall named a specimen from Curaçao as *Voluta musica damula*, which when compared with other specimens from Curaçao appears to be a narrower and higher spired form which otherwise shares the same morphology. Plate 4 illustrates Dall's holotype of *V. musica damula* together with five other specimens from Curaçao, and three specimens from Bonaire. The specimens from Curaçao, denoted as *V. musica damula* are distinct from other populations, and therefore *V. damula* is recognized herein as a full species. The specimens from Bonaire, like those from Aruba exhibit similar degrees of shape, form, and color pattern to the varieties found along the Venezuelan coast, including the form which was named *V. musica guiniaca*.

One of the most distinctive populations in the *Voluta musica* complex is found off the island of Tobago, which was named *Voluta musica typica* by Dall. Plate 5 illustrates nine specimens of *V. musica typica* which all show the distinctive broad shoulders and proportionately large shoulder knobs of this taxon. It may well be that Dall did not mean to describe this as a new taxon, but was in fact referring to the "typical" *V. musica*. However the Tobago population is morphologically significantly different from the Venezuelan coastal population. Dall's manuscript followed the ICZN rules for naming a new taxon, and he denoted a type specimen deposited in the United States National Museum. Consequently, *Voluta typica* is recognized here as a full species.

The *Voluta musica* complex population from Barbados illustrated in Plate 7, was named *Voluta musica carneolata* by Lamarck, and Olsson determined it to be different enough to warrant full species status (Olsson, 1965). While this population shares some superficial

similarities to certain Venezuelan coastal population specimens it is most likely the creamy rose color which leads to confusion. However, *Voluta carneolata* appears to be endemic to Barbados and is confirmed here as a full species.

The *Voluta musica* complex population from Martinique illustrated in Plate 8, was named *Voluta musica thairella* by Lamarck. This population is very distinctive from other members of the *V. musica* complex and is narrower, higher-spired, darkly-patterned, and exhibits a heavily sculpted shoulder. Olsson studied Lamarck's type specimen in the Geneva Museum and referred to *V. thiarella* as a full species (Olsson, 1965). Due to its distinctive form and being endemic to Martinique, *Voluta thiarella* is confirmed here as a full species.

Finally, the author has only seen three specimens from Grenada (illustrated in Plate 9), and none from St. Lucia. However, as expected with isolated island populations, the Grenada specimens share similar morphology, pattern and color with one another, significantly differ from the Venezuelan coastal population, and differ to some degree from the other island populations. Based upon the extensive field work by Verrill the Grenada population may in fact be what was named *Voluta musica plicata* (see Verrill, 1950); more Grenada specimens are needed for study.

Macrophotographs of the protoconchs and early whorls of some specimens in the *Voluta musica* complex are shown on Plate 10. For ease of comparison of the various *V. musica* populations, a single specimen from each population or taxon in the *V. musica* complex is shown on Plate 11. Future studies should focus on obtaining more live collected specimens from each of the separate islands within the geographical distribution of the *V. musica*

complex. This would allow for examination of the protoconchs and early whorls, which have proven to be an important character in volutid studies, as well as conducting thorough molecular studies.

As previously indicated, north of Martinique deep oceanic passages and trenches separate island groups and effectively prevent dispersal of direct developers such as *V. musica* and its sibling species. The author has not seen any substantiated records of live collected *V. musica* specimens from north of Martinique, with merely anecdotal references to specimens being collected from the northern islands of Dominica, Barbuda, St. Kitts, and Puerto Rico.

It is reasonable to conclude that from the Pliocene to the present, with significant sea level fluctuations over geological time, populations of ancestral *V. musica* have become physically isolated on offshore islands, and those populations became genetically isolated, and evolved into closely related allopatric species. Based upon the collective works of Lamarck, Dall, Verrill, Olsson, and Gibson-Smith, and the distinctive morphology, color pattern, isolated geographic locations, ecology and dispersal capabilities of these taxa the author hereby recognizes the following taxa as full species: *Voluta musica*, *V. carneolata*, *V. thiarella*, *V. damula*, and *V. typica*. Further study is needed concerning *V. musica laevigata*, *Voluta musica guiniaca*, and *Voluta musica plicata*.

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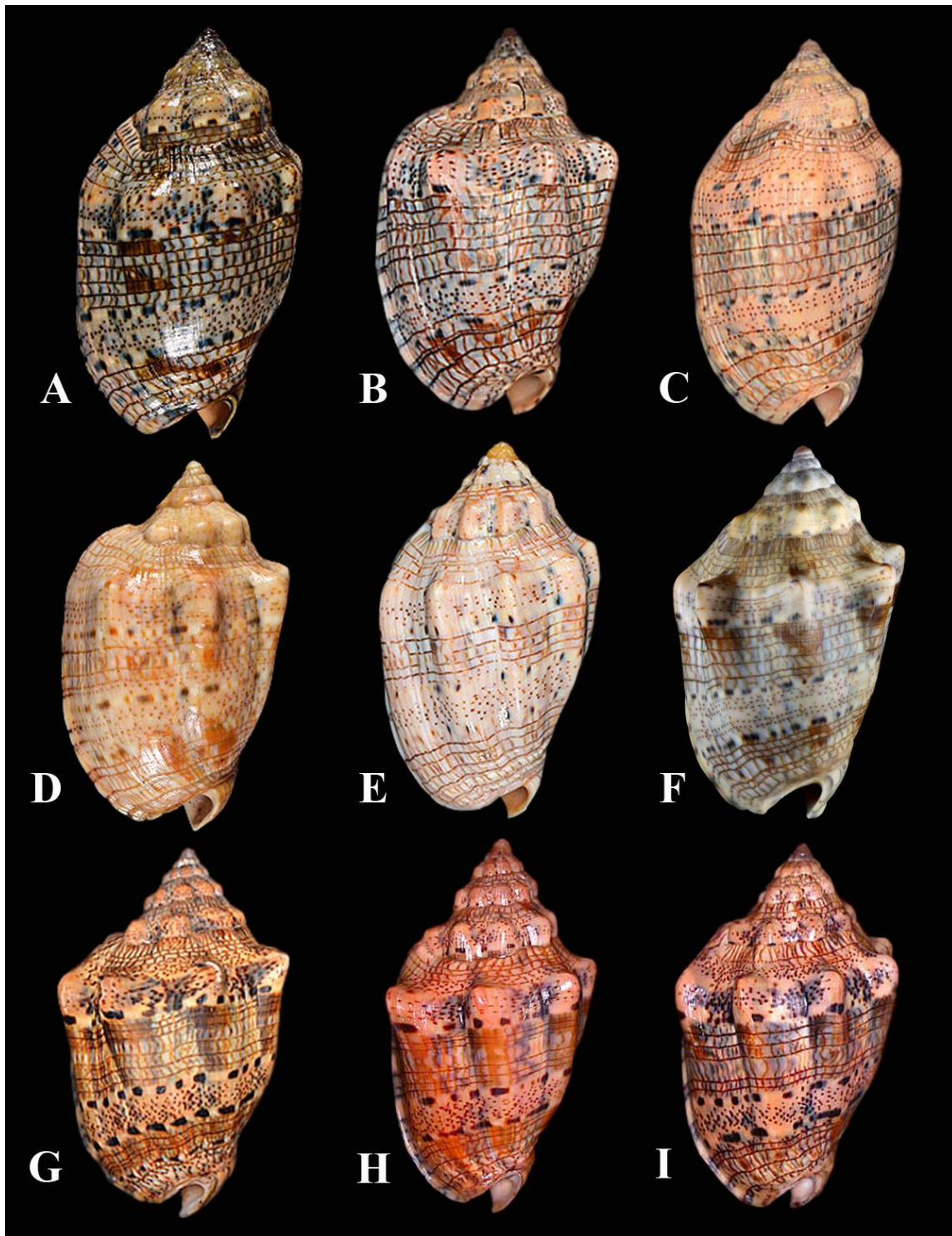


Plate 1. Venezuelan coastal population of *Voluta musica*.

A= *Voluta musica* form *guiniaca*, length 78.8 mm; **B=** *V. musica*, length 77.8 mm; **C=** *V. musica* form *guiniaca*, length 71.5 mm; **D=** *V. musica*, length 64.1 mm; **E=** *V. musica* form *guiniaca*, length 54.6 mm; **F=** *V. musica*, length 73.8 mm; **G=** *V. musica*, length 103.0 mm; **H=** *V. musica*, length 93.7 mm; **I=** *V. musica*, length 99.1 mm.

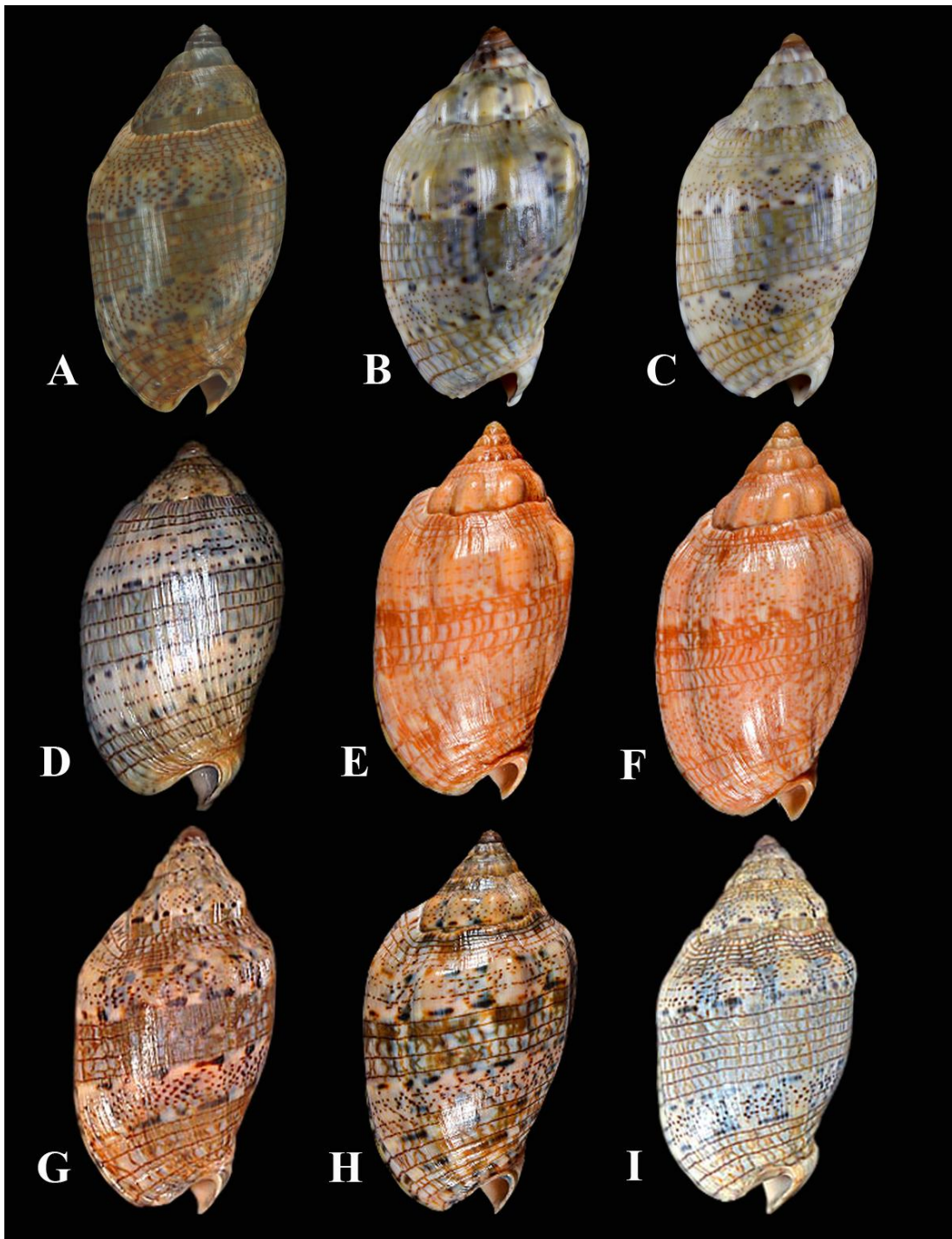


Plate 2. Venezuelan coastal population of *Voluta musica*.

A= *Voluta musica* form *laevigata*, length 60.1 mm; **B=** *V. musica* form *laevigata*, length 59.5 mm; **C=** *V. musica* form *laevigata*, length 50.7 mm; **D=** *V. musica* form *laevigata*, length 41.6 mm; **E=** *V. musica* form *laevigata*, length 59.3 mm; **F=** *V. musica* form *laevigata*, length 60.3 mm; **G=** *V. musica* form *guiniaca*, length 61.9 mm; **H=** *V. musica* form *guiniaca*, length 60.8 mm; **I=** *V. musica* form *guiniaca*, length 64.0 mm.

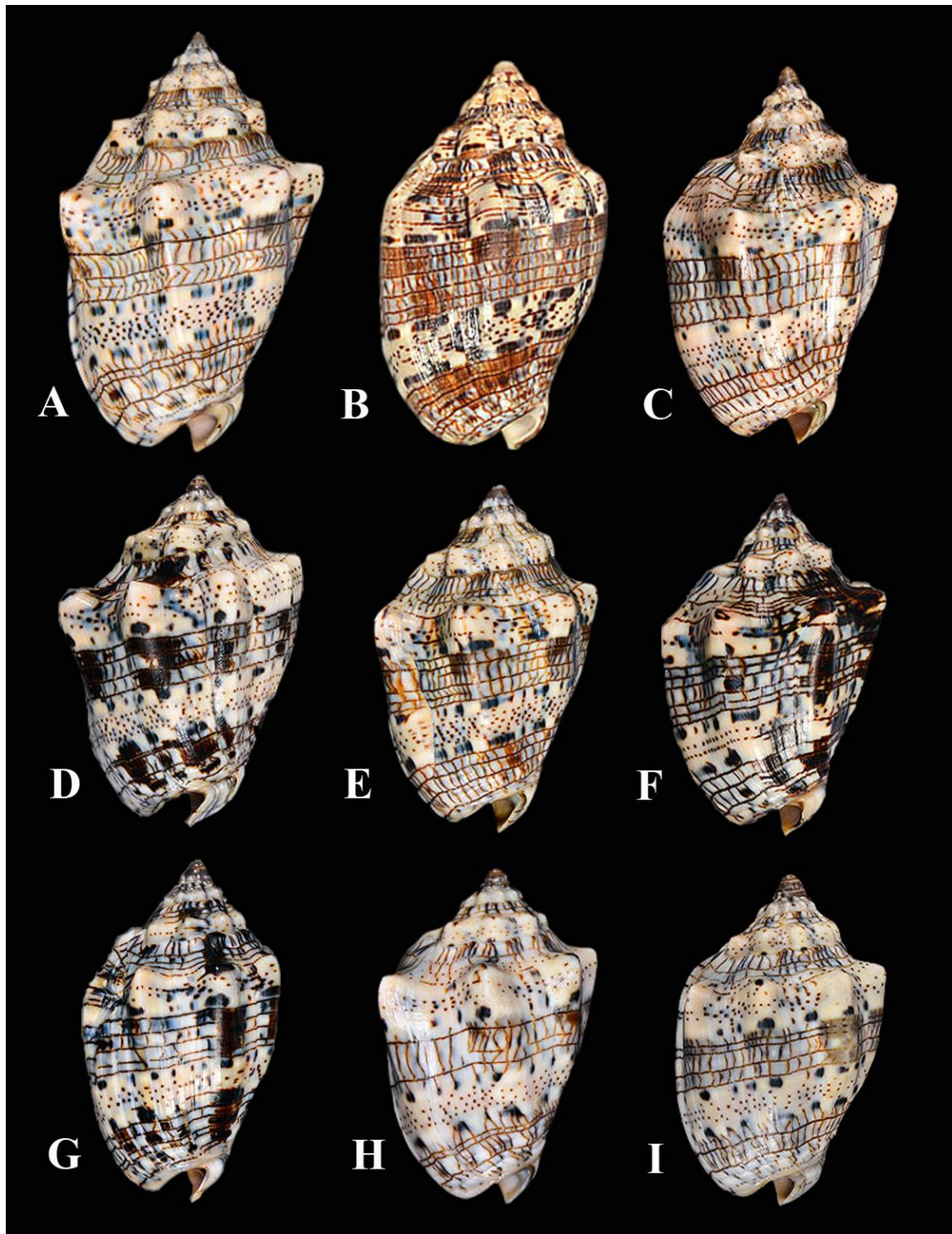


Plate 3. Aruba population of *Voluta musica* complex.

A= *cf. Voluta musica*, length 57.8 mm; **B=** *cf. V. musica*, length 65.5 mm; **C=** *cf. V. musica*, length 52.8 mm; **D=** *cf. V. musica*, length 57.2 mm; **E=** *cf. V. musica*, length 52.8 mm; **F=** *cf. V. musica*, length 48.0 mm; **G=** *cf. V. musica*, length 46.1 mm; **H=** *cf. V. musica*, length 46.1 mm; **I=** *cf. V. musica*, length 46.0 mm.

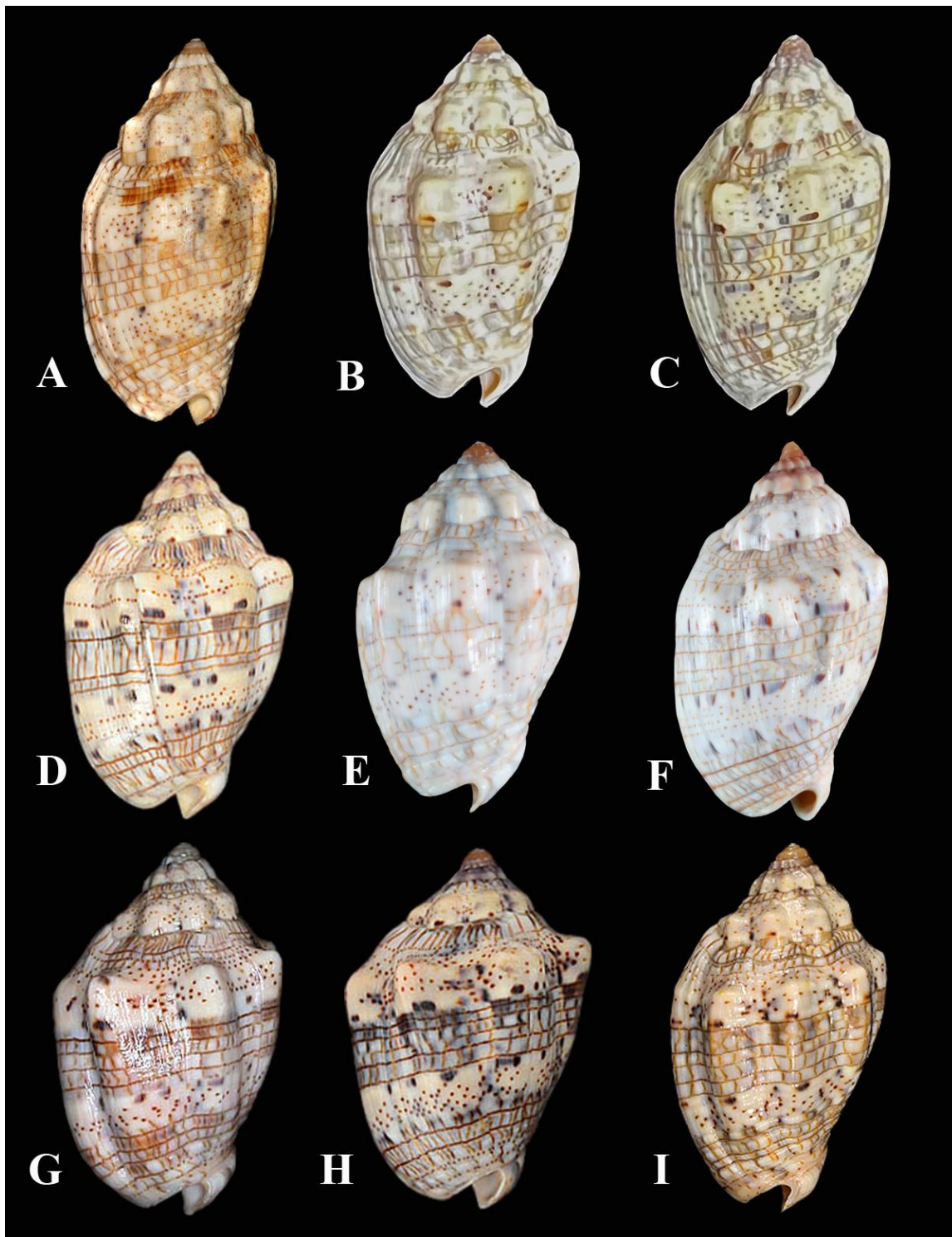


Plate 4. Curaçao and Bonaire populations of *Voluta musica* complex.

Curaçao population: A= *Voluta damula*, holotype USNM No. 24929, length 44.4 mm; B= *V. damula*, length 48.0 mm; C= *V. damula*, length 52.0 mm; D= *V. damula*, length 47.5 mm; E= *V. damula*, length 35.9 mm; F= *V. damula*, length 57.6 mm; **Bonaire population:** G= cf. *V. musica*, length 51.4 mm; H= cf. *V. musica*, length 39.9 mm; I= cf. *V. musica*, length 38.4 mm.

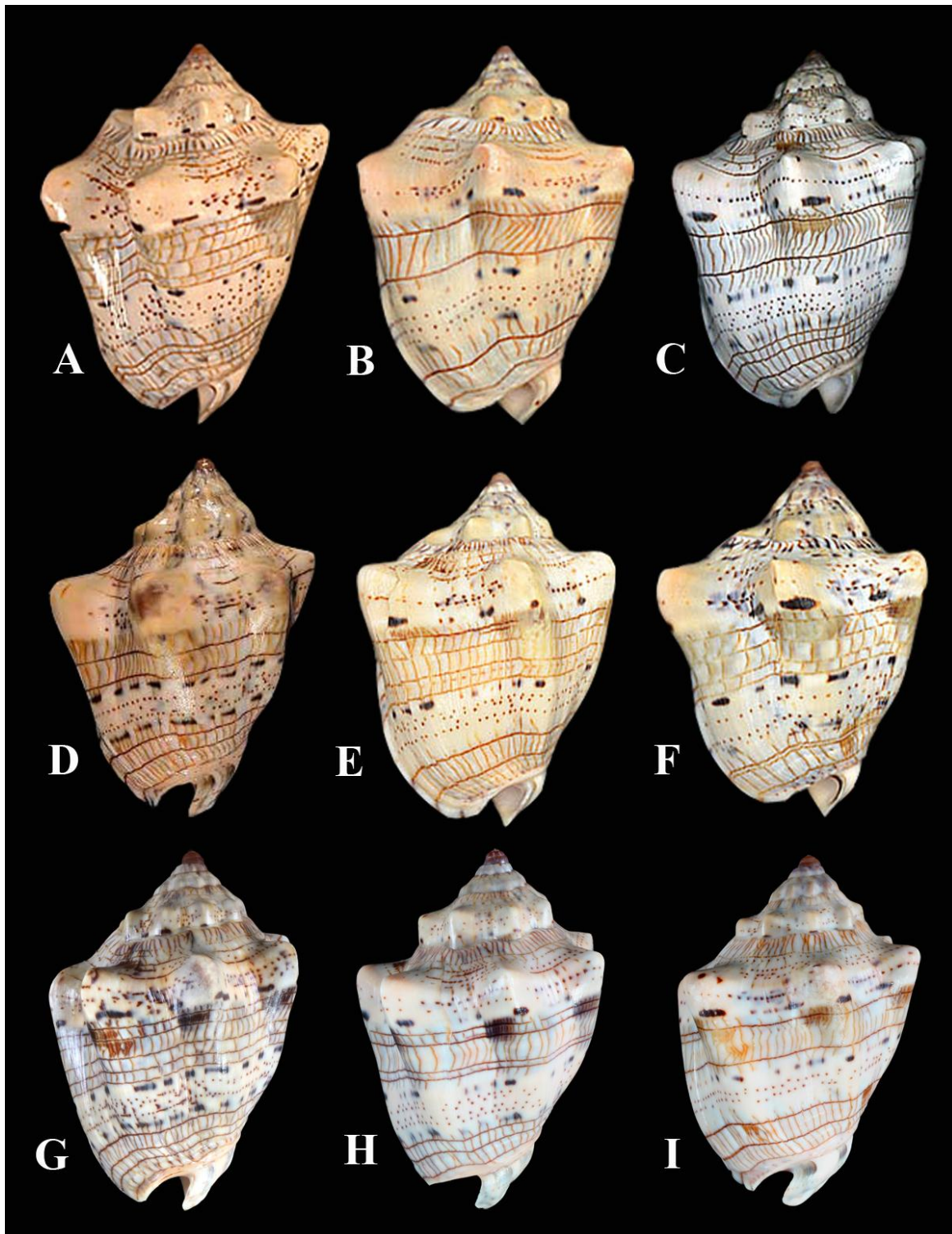


Plate 5. Tobago population of *Voluta musica* complex.

A= *Voluta typica*, length 71.4 mm; **B**= *V. typica*, length 65.0 mm; **C**= *V. typica*, length 64.2 mm; **D**= *V. typica*, length 63.0 mm; **E**= *V. typica*, length 57.2 mm; **F**= *V. typica*, length 55.4 mm; **G**= *V. typica*, length 63.6 mm; **H**= *V. typica*, length 63.7 mm; **I**= *V. typica*, length 58.9 mm.

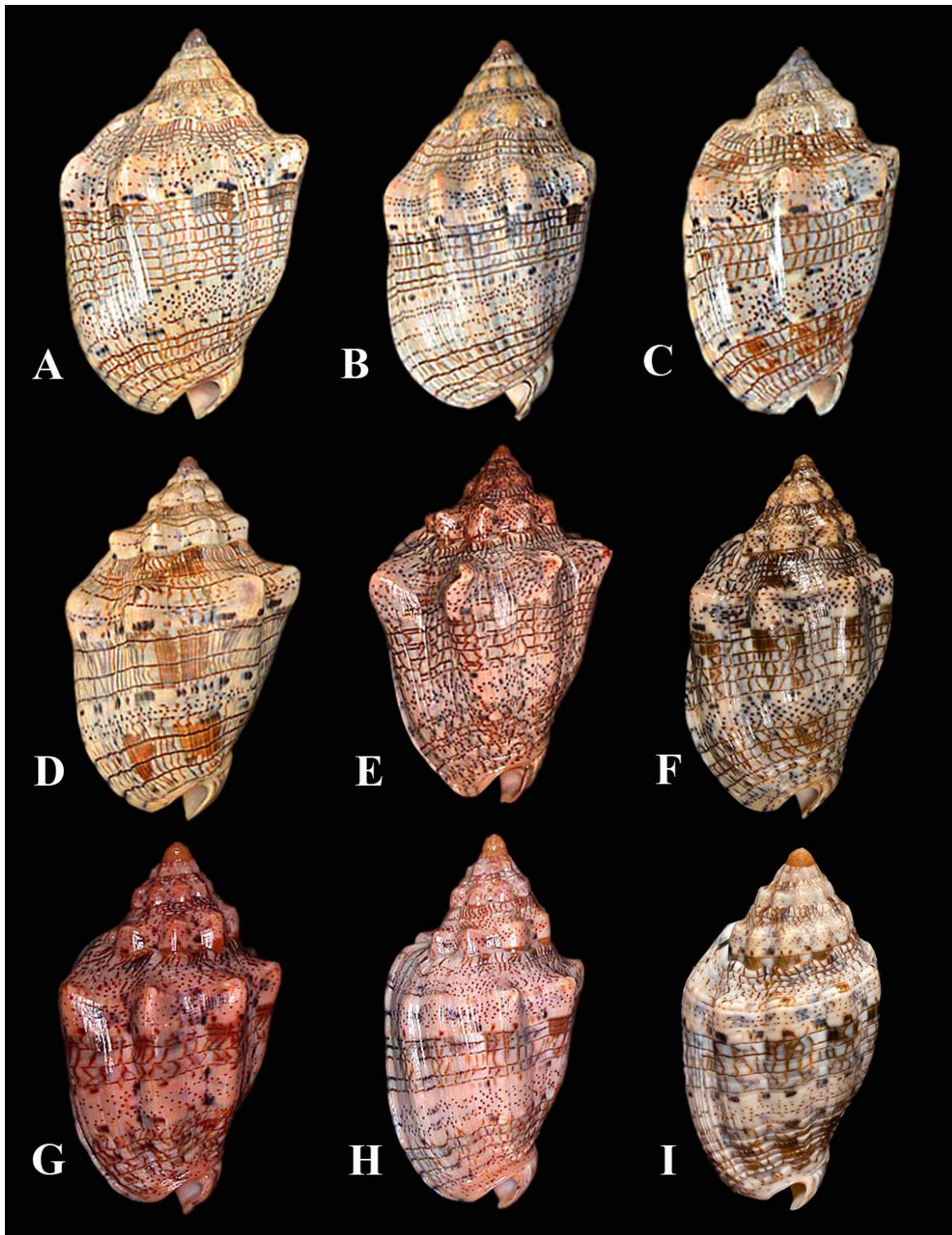


Plate 6. St. Vincent population of *Voluta musica* complex.

A= *cf. Voluta musica*, length 79.5 mm; **B**= *cf. V. musica*, length 76.6 mm; **C**= *cf. V. musica*, length 75.1 mm; **D**= *cf. V. musica*, length 79.8 mm; **E**= *cf. V. musica*, length 63.7 mm; **F**= *cf. V. musica*, length 51.8 mm; **G**= *cf. V. musica*, length 59.2 mm; **H**= *cf. V. musica*, length 72.0 mm; **I**= *cf. V. musica*, length 61.5 mm.

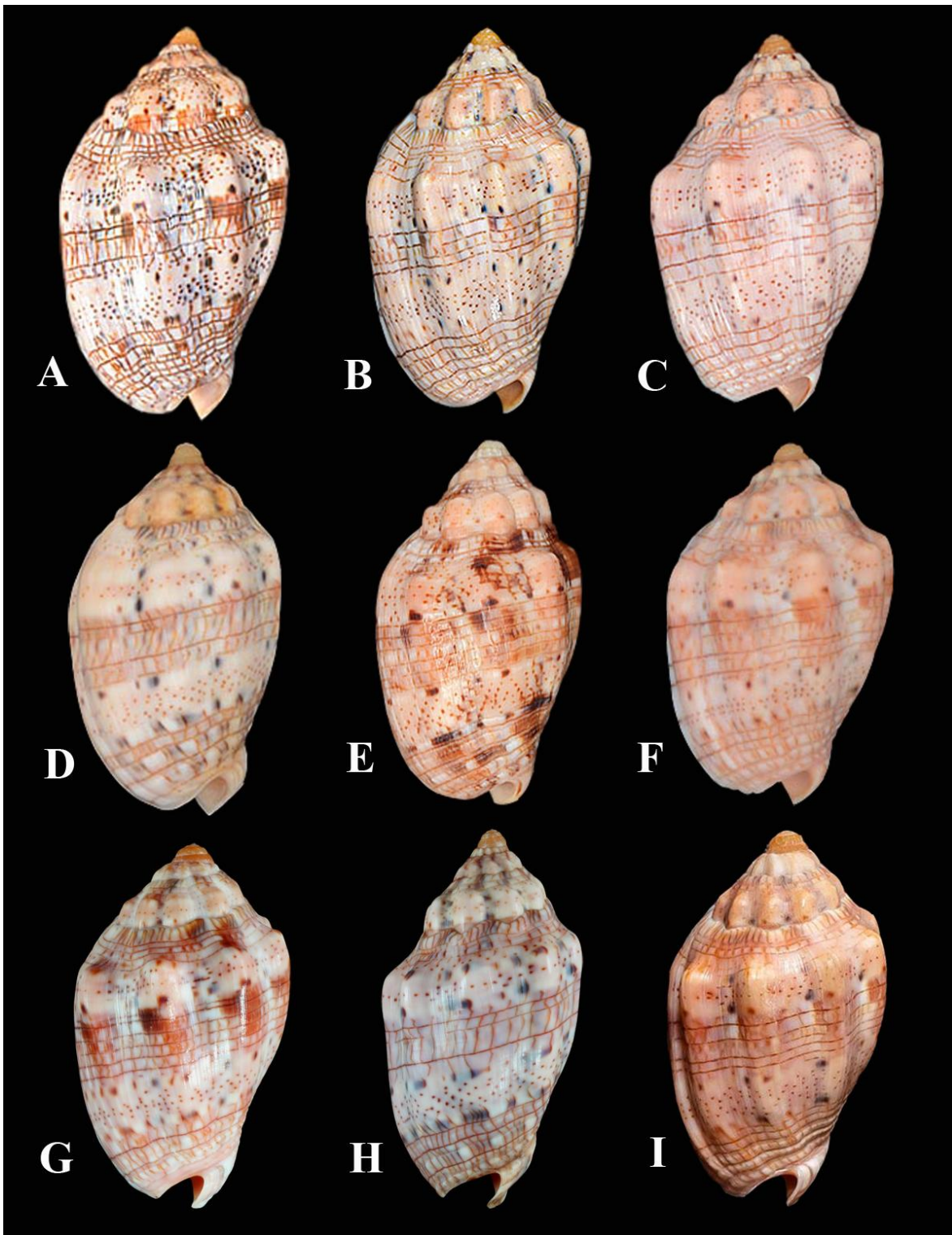


Plate 7. Barbados population of *Voluta musica* complex.

A= *Voluta carneolata*, length 60.2 mm; B= *V. carneolata*, length 54.6 mm; C= *V. carneolata*, length 48.8 mm; D= *V. carneolata*, length 45.4 mm; E= *V. carneolata*, length 44.8 mm; F= *V. carneolata*, length 44.8 mm; G= *V. carneolata*, length 47.0 mm; H= *V. carneolata*, length 56.8 mm; I= *V. carneolata*, length 47.5 mm.

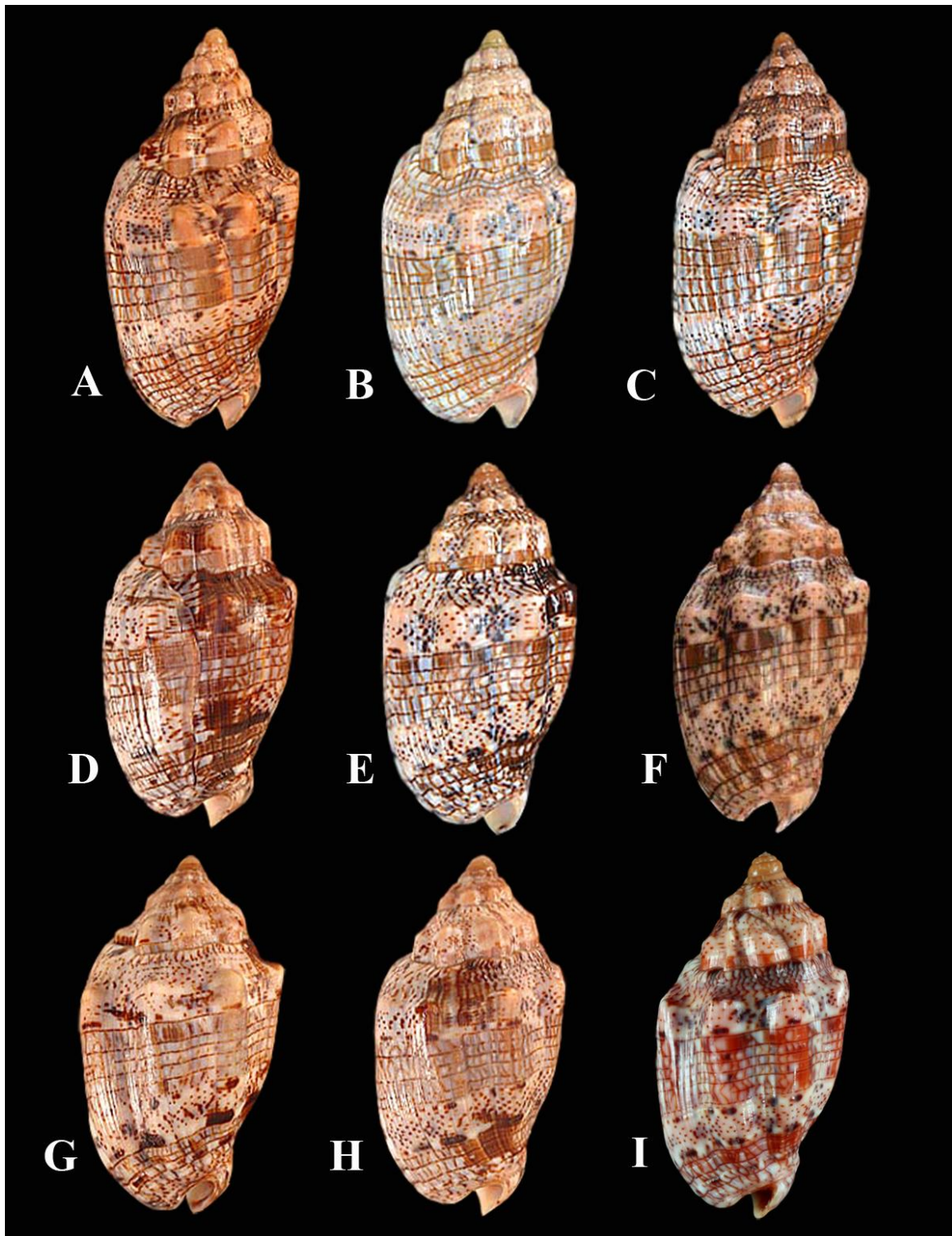


Plate 8. Martiniq population of *Voluta musica* complex.

A= *Voluta thiarella*, length 75.0 mm; **B=** *V. thiarella*, length 66.0 mm; **C=** *V. thiarella*, length 62.3 mm; **D=** *V. thiarella*, length 52.7 mm; **E=** *V. thiarella*, length 51.7 mm; **F=** *V. thiarella*, length 50.2 mm; **G=** *V. thiarella*, length 50.1 mm; **H=** *V. thiarella*, length 48.4 mm; **I=** *V. thiarella*, length 52.3 mm.

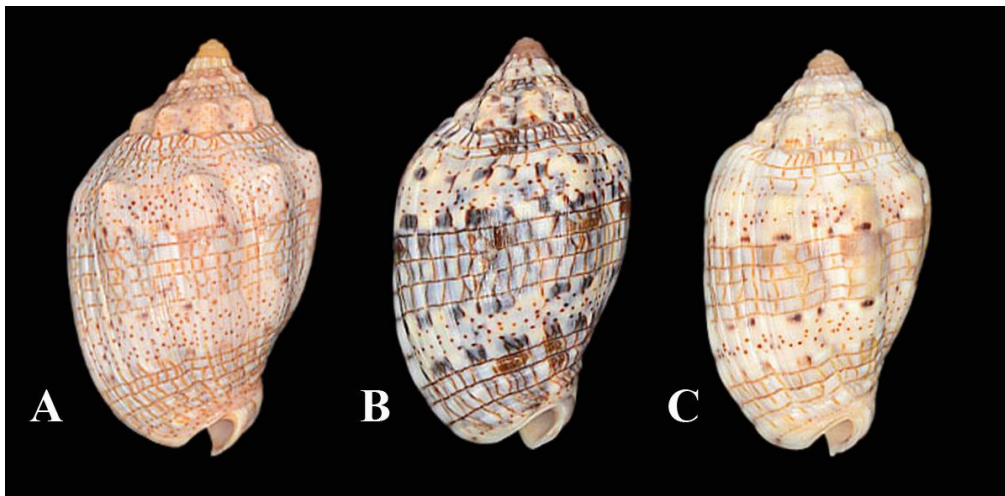


Plate 9. Grenada population of *Voluta musica* complex.

A= *cf. Voluta musica*, length 49.4 mm; B= *cf. V. musica*, length 41.0 mm; C= *cf. V. musica*, length 37.5 mm.

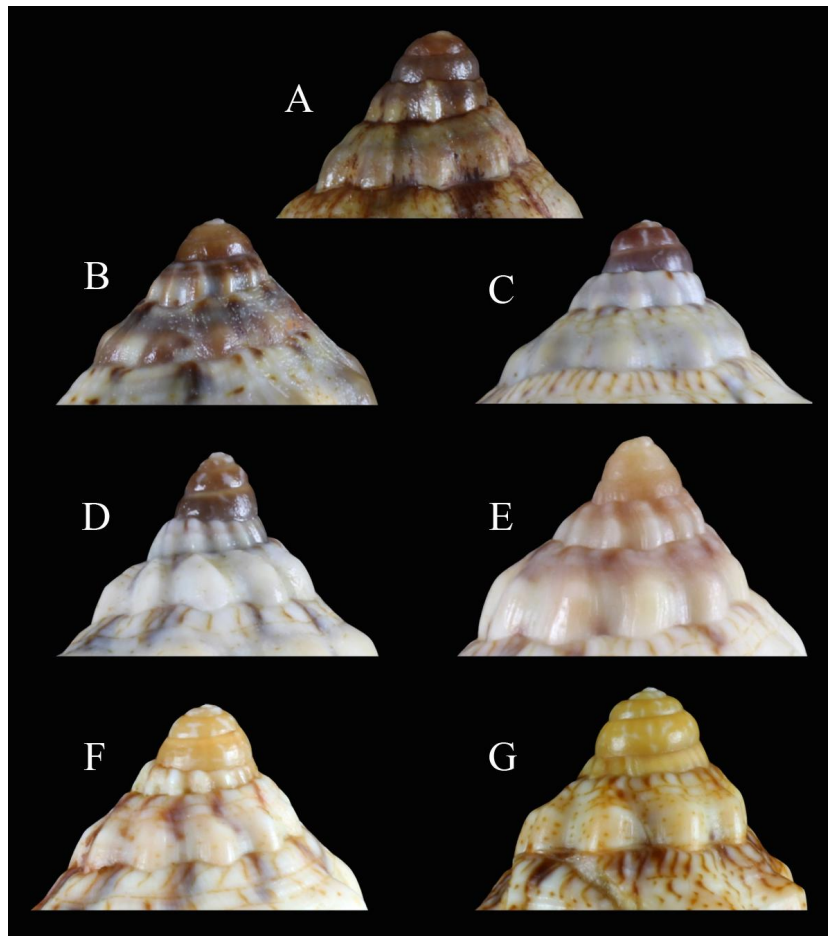


Plate 10. Macrophotographs of protoconchs and early whorls of *Voluta musica* complex.

A= *Voluta musica*; B= *Voluta musica* form *laevigata*; C= *V. typica*; D= *V. musica*, Aruban population; E= *V. damula*; F= *V. carneolata*; G= *V. thiarella*.

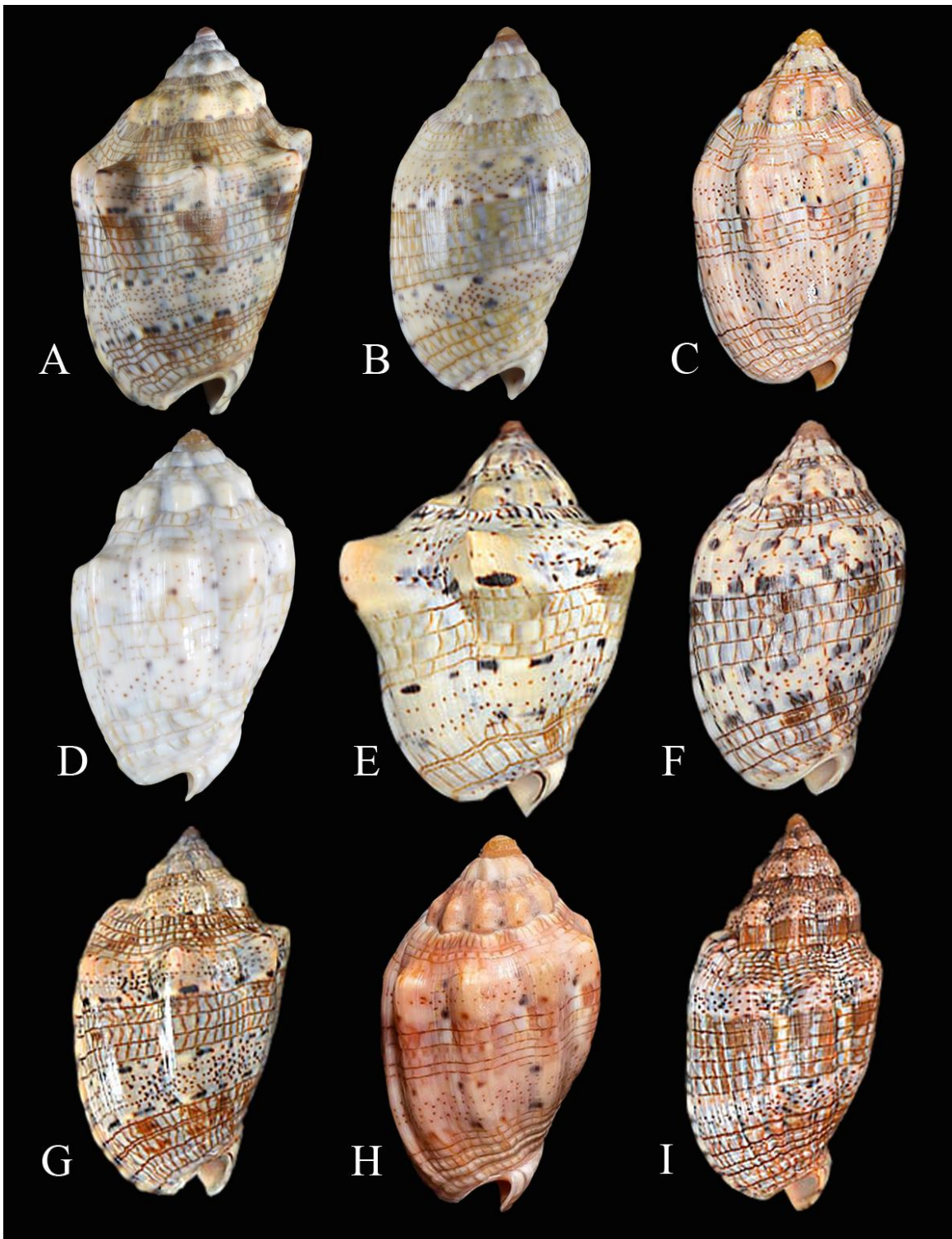


Plate 11. Populations of the *Voluta musica* complex.

A= *Voluta musica* (Venezuelan coast); **B=** *Voluta musica* form *laevigata* (Gulf of Venezuela and Venezuelan coast); **C=** *Voluta musica* form *guiniaca* (Venezuelan coast); **D=** *Voluta damula* (Curaçao); **E=** *Voluta typica* (Tobago); **F=** *Voluta musica* cf. *plicata* (Grenada); **G=** *Voluta musica* (St. Vincent population); **H=** *Voluta carneolata* (Barbados); **I=** *Voluta thiarella* (Martinique).