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**A comparison of adaptive radiation in Conidae and Conilithidae (Gastropoda: Conoidea) in the Eastern and Western Atlantic, together with an iconography of the conilithid genus *Jaspidiconus***

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**ABSTRACT** Comparison is made between two diverse faunas of conoidean gastropods in the tropical western Atlantic and eastern Atlantic, which have undergone dramatic adaptive radiation in a relatively short geological period. Hypothetical speciation processes of these groups are discussed, compared and contrasted. A complete iconography of the living species of *Jaspidiconus* together with a discussion of biogeographic regions is made to place these species hypotheses in their environmental and ecological context, together with a discussion of the requirement of total evidence and suggestions for further studies.

**KEYWORDS** Adaptive radiation, evolution, allopatric speciation, sympatric speciation, species flock, iconography, *Jaspidiconus*, *Coltroconus*, *Africonus*, Conidae, Conilithidae.

## INTRODUCTION

Conoidean gastropods and their associated conotoxins have rapidly evolved to fill diverse ecological niches. There are over 760 living species of cones, and an estimated 10,000 living species of turrids (Bouchet & Lozouet, 2004; Tucker, 2004; Pulliandre, *et al.*, 2014; Tucker & Tenorio, 2013). This remarkable evolutionary radiation is believed to be due to the dietary specialization and the predator-prey co-evolution of neurotoxins used by conoidean gastropods to subdue their prey (Taylor, *et al.*, 1980; Duda & Palumbi, 2004; Chang & Duda, 2012; Olivera, *et al.*, 2012; Pulliandre, *et al.*, 2014). A comparison of the adaptive radiation of two diverse groups of conoidean gastropods is presented.

## DISCUSSION

Species flocks or swarms are rarely reported from marine environments. A species “flock” is defined as an endemic and monophyletic assemblage of taxa that rapidly evolved in a

small defined geographic area with no obvious barriers to dispersal (Duda & Rolan, 2005). Species flocks tend to occur in relatively closed systems following colonization of an isolated area. There are over 70 species of *Africonus* which have evolved in the last few million years that are restricted to, the Cape Verde archipelago (Tucker & Tenorio, 2013). These gastropods fit the definition of a species flock with species that originated in limited parts of the archipelago. In some cases, species radiations occurred within a single island (Duda & Rolan, 2005).

Allopatric speciation or geographic speciation occurs when biological populations of the same species become isolated from each other to an extent that interferes with or prevents breeding and genetic exchange. Over time the two populations undergo genotypic or phenotypic divergence as a result of different selective pressures, mutations, or genetic drift, evolving distinctly different characteristics to the point where the two populations are unable to successfully mate with one another (Lande,

1980; Hoskin, *et al.*, 2005). This is based upon Ernst Mayr's "biological species concept" (BSC) which emphasizes reproductive isolation for determining species (Mayr, 1963). The BSC states: "A species is defined as a population or group of populations whose members have the potential to interbreed with one another in nature and to produce viable offspring, but cannot produce viable, fertile offspring with members of other species." (Mayr, 1970). This definition of species does not exclude the occurrence of hybrids, albeit the definition assumes that such hybrids would be sterile and unable to produce viable offspring; cf. the Liger, a hybrid offspring of a male lion (*Panthera leo*) and a female tiger (*Panthera tigris*) which often is fertile (Mott, 2005). Hybridization in the mollusca is believed to be an uncommon event, with recognized hybrids in the Haliotidae and Strombidae; whether such hybrids are fertile or sterile is unknown (Owen, *et al.*, 1971; Kronenberg, 2008). Nevertheless, fertile hybrids challenge the very definition of what constitutes a species.

Sympatric speciation occurs when a new species evolves from an ancestral species while inhabiting the same geographic area; this is a splitting event, *i.e.* at least two species are the end product. Sympatric speciation is thought to be an uncommon but plausible process by which two or more breeding populations of the same species become reproductively isolated and therefore subject to different causal events such as genetic drift due to different mutations, and different selective pressures (Kondrashov, *et al.*, 1999; Fitzpatrick, *et al.*, 2008). While sympatric speciation is controversial and it has been posited that different microhabitats or niches, mating signals or timing, among groups in a species can lead to reproductive isolation (Jiggins, 2006). In other words, if such speciation is truly allopatric, then it is a matter of scale. There are, however, true instances of

sympatric speciation, polyploidy in plants and another mode seen among some insects where breeding behavior is immediately modified. This is at the core of adaptive radiation.

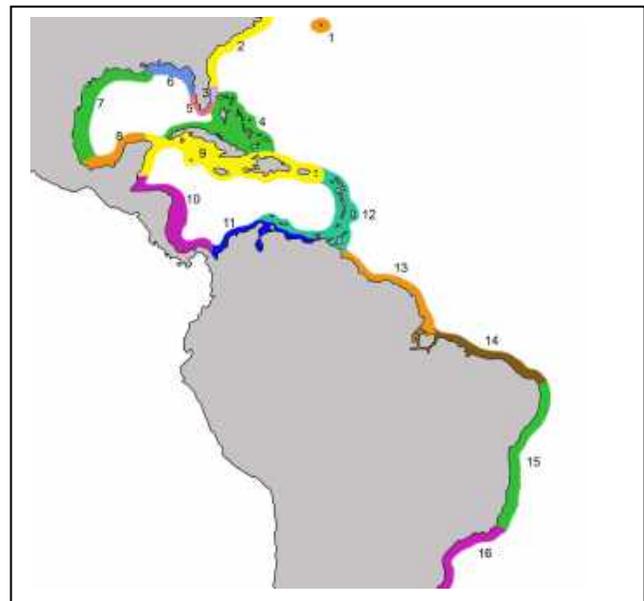
Isolated marine faunas do not typically occur because of the lack of barriers to restrict or define geographic areas within oceans (Palumbi, 1994; Duda & Rolan, 2005). Nonetheless endemic species do occur, and some areas exhibit a high degree of endemism. The majority of conid (Conidae and Colilithidae) species, about 75%, undergo a planktonic development in their life history (Kohn & Perron, 1994), however the Cape Verde endemic species in the genus *Africonus*, and the Western Atlantic species in the conilithid genus *Jaspidiconus* (described by Petuch, 2003), have lechithotrophic benthic development, *i.e.* they are direct developers with no planktonic larval stage. Juveniles hatch directly from egg capsules and dispersal is limited to how far an individual can crawl in its lifetime within their habitat (Trovao, *et al.*, 1990; Duda & Rolan, 2005; Petuch & Myers, 2014). Distances between suitable shallow water habitats on different islands in the Caribbean isolated both by many miles and inhospitable depths, combined with direct development hypothetically severely restrict gene flow between islands. The resulting isolation of breeding populations can facilitate evolution either by adaptive radiation, genetic drift, or fixation of unique traits in a founder population. Endemic species of conoidean gastropods are believed to be relatively common throughout the Western Atlantic, and constitute a significant part of the quantitative analysis of what comprises a marine faunal province or subprovince (Petuch, 2013).

While the Cape Verde archipelago genus *Africonus* has been described as a species flock, some scientists have been reluctant to recognize

the allopatric speciation of the Western Atlantic conids in the genus *Jaspidiconus* either via adaptive radiation, genetic drift, or founder population. Some researchers believe that the apparent biodiversity of the genus is represented in the single type species *J. jaspideus* s.s. (Gmelin, 1791), which they believe to be highly variable (Tucker, 2012; Kohn, 2014, synonymizing most species and recognizing only the single genus *Conus*). This single species hypothesis does not accept the premise that allopatric speciation of *Jaspidiconus* has occurred in the Caribbean throughout geological time.

The tropical and subtropical Western Atlantic Region from Cape Hatteras, North Carolina, United States, south to Mar del Plata, Argentina, encompasses three marine faunal regions (the Carolinian, Caribbean, and Brazilian), each of which has its own separate fauna of conoidean gastropods (Petuch, 2013; Petuch & Myers, 2014a). The conolithid genus *Jaspidiconus* in these marine faunal provinces is thought to include at least 60 species, approximately one-third of which are still undescribed (Petuch, personal communication). *Jaspidiconus* have proportionately large paucispiral protoconchs, have lechithotrophic benthic development, never dispersing far from where they hatch (Petuch, 2013; Petuch & Myers, 2014a). Given the fact that *Jaspidiconus* species have lechithotrophic benthic development, inhabit relatively shallow water, they have limited dispersal capabilities, a high degree of endemism among the myriad islands and coral cays throughout these provinces is believed to be the result (Petuch, 2013; Petuch & Myers, 2014a). The Holocene species in *Coltroconus* are believed to have recently evolved from *Jaspidiconus*, and are included as part of the radiation of this successful group (Petuch, 2013; Petuch & Myers, 2014b included *Coltroconus* as a subgenus of *Jaspidiconus*).

Only one species of *Jaspidiconus* has a broad distribution throughout these three major provinces, *J. mindanus* (Hwass in Bruguiere, 1792), which is found from the Floridian Subprovince of the Carolinian Province south through the Brazilian Province; the remaining species are either endemics, have restricted ranges, or are far southern coastal species such as *J. pusio* or *J. pusillus*. *J. mindanus* may have geographically localized forms or subspecies including: *J. mindanus agassizii* (Dall, 1886), *J. mindanus bermudensis* (Clench, 1942), *J. mindanus karinae* (Nowell-Usticke, 1968), and *J. mindanus lymani* (Clench, 1942); these localized forms or subspecies may reflect the beginning stages of speciation. An iconography of the living *Jaspidiconus* species hypotheses broken down by marine faunal provinces and subprovinces from north to south follows.



**Figure 1.** Tropical Western Atlantic biogeographical zones: 1. Bahamian Subprovince, 2. Georgian Subprovince, 3. Palm Beach Provinciatone (of the Georgian Subprovince), 4. Bermudan Subprovince, 5. Floridian Subprovince, 6. Suwannean Subprovince, 7. Texan Subprovince, 8. Yucatecan Subprovince, 9. Antillean Subprovince, 10. Nicaraguan Subprovince, 11. Venezuelan Subprovince, 12. Grenadian Subprovince, 13. Surinamian Subprovince, 14. Cearaian Subprovince, 15. Bahian Subprovince, 16. Paulinian Subprovince.

## ICONOGRAPHY OF LIVING *JASPIDICONUS*

### Carolinian Province.

#### Georgian Subprovince

*J. pfluegeri* Petuch, 2003 (North Carolina to Palm Beach, and also Middle Florida Keys)

#### Floridian Subprovince

*J. fluviamaris* Petuch & Sargent, 2011 (Palm Beach to Dry Tortugas)

*J. pealii* (Green, 1830) (endemic to Florida Keys)

*J. vanhyningi* (Rehder, 1944) (Palm Beach to Florida Keys)



**Figure 2. Georgian and Floridian Subprovinces:** A = *Jaspidiconus pfluegeri* Petuch, 2003 holotype; B = *J. fluviamaris* Petuch & Sargent, 2011 holotype; C = *J. pealii* (Green, 1830) from the David P. Berschauer Collection (collected by Edward Petuch, Middle Torch Key, Florida); D = *J. vanhyningi* (Rehder, 1944) holotype.

#### Suwannean Subprovince

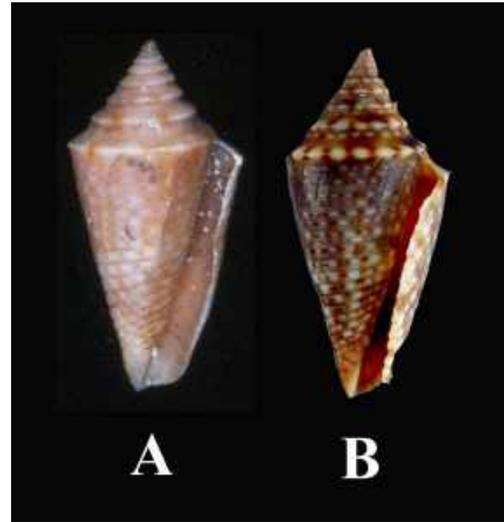
*J. stearnsii* (Conrad, 1869) (endemic to coastal Suwannean Subprovince)

#### Texan Subprovince

None

#### Yucatanean Subprovince

Yet unnamed species



**Figure 3. Suwannean Subprovince:** A = *Jaspidiconus stearnsii* (Conrad, 1869) holotype; B = *J. stearnsii* (Conrad, 1869) from the Alexander Medvedev Collection.

### Caribbean Province.

#### Bermudan Subprovince

*J. mindanus bermudensis* (Clench, 1942) (endemic to Bermuda)

#### Bahamian Subprovince

*J. branhamae* (Clench, 1953) (endemic to the Abacos)

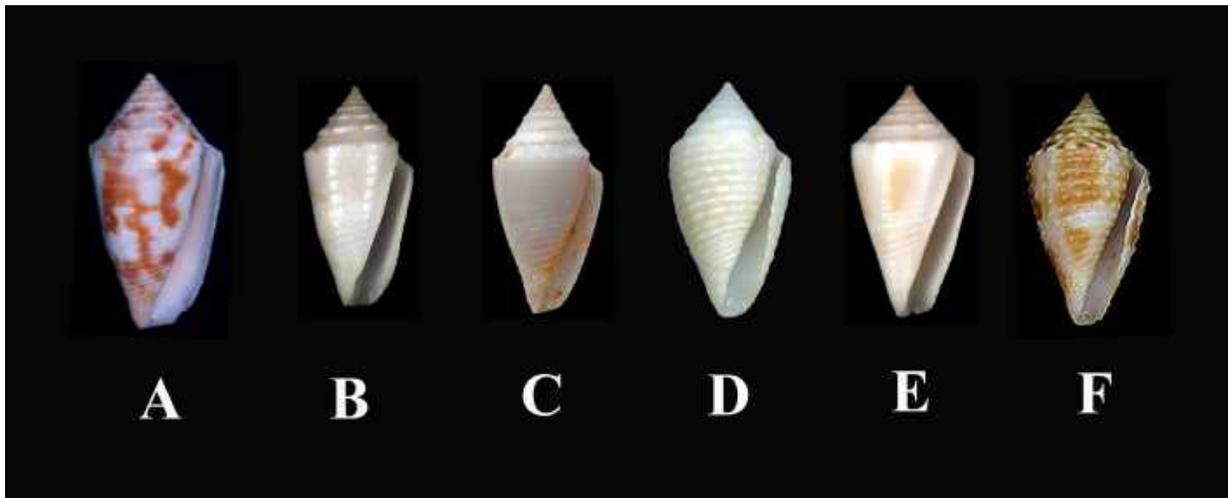
*J. exumaensis* Petuch, 2013 (endemic to Exuma Sound)

*J. herndli* Petuch & Myers, 2014a (endemic to S. Bimini Chain, Great Bahama Bank)

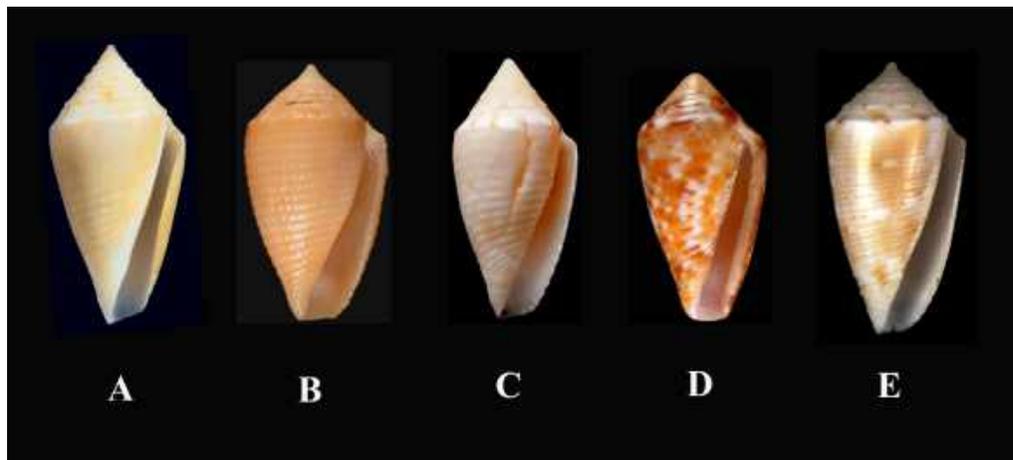
*J. nodiferus* (Kiener, 1847) (Bahamas to Lesser Antilles)

*J. oleiniki* Petuch, 2013 (endemic to the Bimini Chain)

*J. verrucosus* (Hwass in Bruguiere, 1792) (Bahamas to Lesser Antilles)



**Figure 4. Bahamian Subprovince:** A= *Jaspidiconus branhamae* (Clench, 1953) holotype; B= *J. exumaensis* Petuch, 2013 holotype; C= *J. herndli* Petuch & Myers, 2014 holotype; D= *J. nodiferus* (Kiener, 1847) from the Paul Kersten Collection; E= *J. oleiniki* Petuch, 2013 holotype; F= *J. verrucosus* (Hwass in Bruguiere, 1792) from the Paul Kersten Collection.



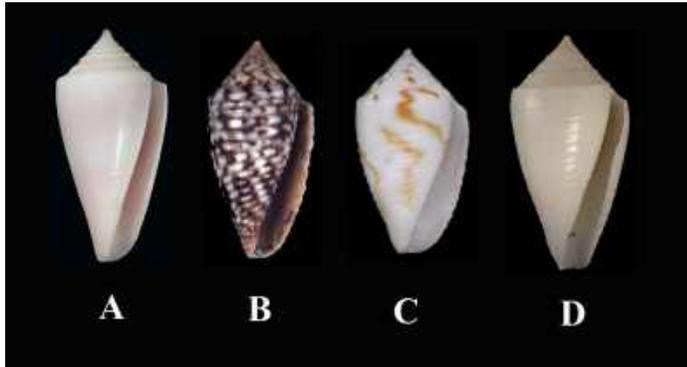
**Figure 5. Antillean Subprovince:** A= *Jaspidiconus agassizii* (Dall, 1886) lectotype; B= *J. anaglypticus* (Crosse, 1865) holotype; C= *J. berschaueri* Petuch & Myers, 2014 holotype; D= *J. duvali* (Bernardi, 1862) holotype; E= *J. mackintoshi* Petuch, 2013 holotype.

#### Antillean Subprovince

- J. agassizii* (Dall, 1886) (endemic to St. Croix, US Virgin Islands)
- J. anaglypticus* (Crosse, 1865) (endemic to Puerto Rico)
- J. berschaueri* Petuch & Myers, 2014a (endemic to St. Maartin Island)
- J. duvali* (Bernardi, 1862) (endemic to Guadalupe)
- J. mackintoshi* Petuch, 2013 (endemic to the Virgin Islands)

#### Nicaraguan Subprovince

- J. alexandremonteiroi* Cossignani, 2014 (endemic to Cayos Miskitos, Nicaragua)<sup>A</sup>
- J. allamandi* Petuch, 2103 (endemic to Roatan Island)
- J. roatanensis* Petuch & Sargent, 2011 (endemic to Roatan Island)
- J. sargenti* Petuch, 2013 (endemic to Roatan Island)



**Figure 6. Nicaraguan Subprovince:** A= *Jaspidiconus alexandremonteiroi* Cossignani, 2014<sup>Δ</sup> holotype; B= *J. allamandi* Petuch, 2013 holotype; C= *J. roatanensis* Petuch & Sargent, 2011 holotype; D= *J. sargenti* Petuch, 2013 holotype.

### Venezuelan Subprovince

- J. acutimarginatus* (Sowerby, 1866)  
(coastal along Colombia to Venezuela)  
*J. jaspideus* (Gmelin, 1791) (coastal  
along Colombia to Venezuela)



**Figure 7. Venezuelan Subprovince:** A= *Jaspidiconus acutimarginatus* (Sowerby, 1866) holotype; B= *J. jaspideus* (Gmelin, 1791) neotype.

### Grenadian Subprovince

- J. arawak* Petuch & Myers, 2014a  
(endemic to Central Grenadine Islands)  
*J. duvali* (Bernard, 1862) (endemic to  
Guadalupe)

*J. jaspideus* (Gmelin, 1791) (neotype is  
from Monos Island, Trinidad;

Grenadines to Tobago)

*J. pusio* (Hwass in Bruguiere, 1792)  
(Grenada to northern Brazil)

### Surinamian Subprovince

*J. pusio* (Hwass in Bruguiere, 1792)  
(Grenada to northern Brazil)

### Brazilian Province.

#### Cearaian Subprovince

*J. damaso*i Cossignani, 2007 (endemic  
to Ceara coast, Brazil)

*J. damasomonteiroi* Petuch & Myers,  
2014 (endemic to Ceara coast and  
offshore Canopus Bank, Brazil)

*J. pusio* (Hwass in Bruguiere, 1792)  
(Grenada to Brazil)

*J. pusillus* (Lamarck, 1810) (endemic  
to Brazilian Province)

#### Bahian Subprovince (a localized species swarm reflecting adaptive radiation)

*J. (Coltroconus) bodarti* Coltro, 2004  
(endemic to Abrolhos Platform)

*J. (C.) deluca*i Coltro, 2004 (endemic  
to Abrolhos Platform)

*J. (C.) henrique*i (Petuch & Myers,  
2014a) (endemic to Royal Charlotte  
Bank, Abrolhos Platform, Brazil)

*J. (C.) iansa* (Petuch, 1979) (endemic  
to Abrolhos Platform)

*J. (C.) schirrmeister*i Coltro, 2004  
(endemic to Abrolhos Platform)

*J. ericmonnieri* Petuch & Myers, 2014a  
(endemic to Bahian Subprovince,  
Brazil)

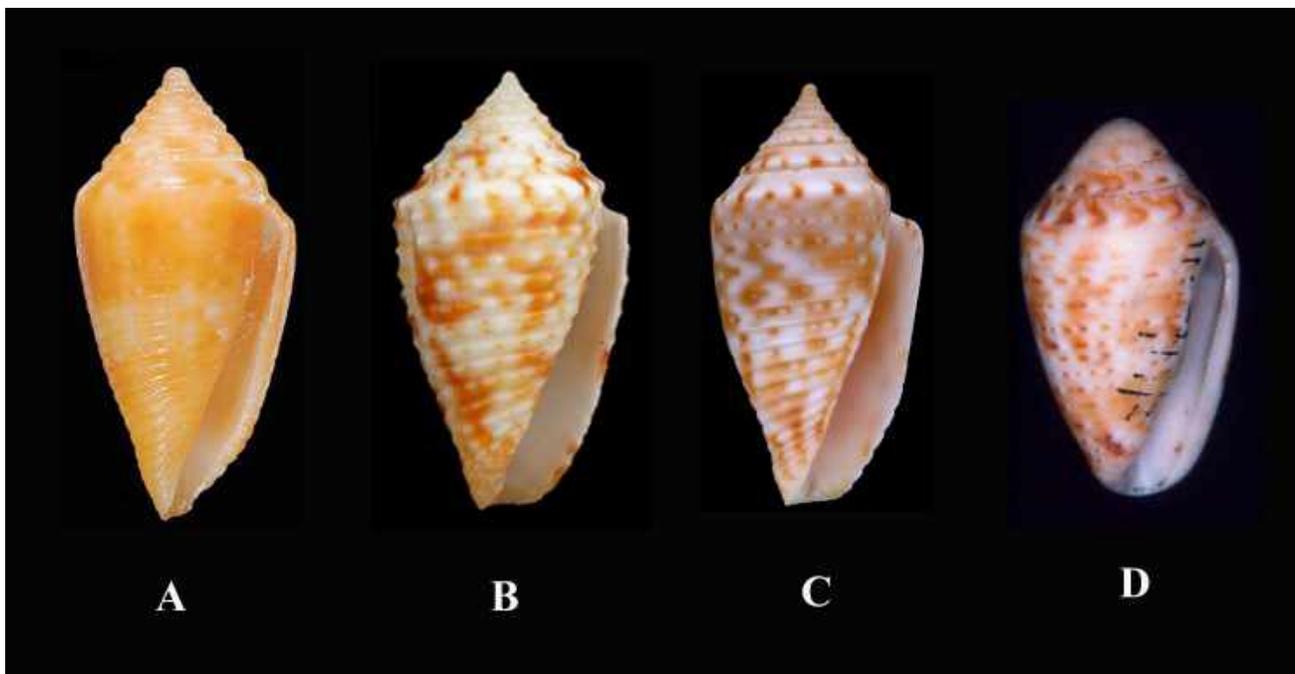
*J. henckesi* Coltro, 2004 (endemic to  
Todos os Santos Bay, Brazil)

*J. marinae* Petuch & Myers, 2014b  
(endemic to Porto Itaparica Island,  
Brazil)

<sup>Δ</sup> See Note on page 110, left margin



**Figure 8. Grenadian Subprovince:** **A**= *Jaspidiconus arawak* Petuch & Myers, 2014 holotype; **B**= *J. duvali* (Bernard, 1862) holotype; **C**= *J. jaspideus* (Gmelin, 1791) neotype; **D**= *J. pusio* (Hwass in Bruguiere, 1792) from the André Poremski Collection.



**Figure 9. Cearaian Subprovince:** **A**= *Jaspidiconus damasoi* Cossignani, 2007 holotype; **B**= *J. damasomonteiroi* Petuch & Myers, 2014 holotype; **C**= *J. pusio* (Hwass in Bruguiere, 1792) from the André Poremski Collection; **D**= *J. pusillus* (Lamarck, 1810) lectotype.



**Figure 10. Bahian Subprovince:** A= *Jaspidiconus (Coltroconus) bodarti* Coltro, 2004 holotype; B= *J. (C.) delucaii* Coltro, 2004 holotype; C= *J. (C.) henriquei* (Petuch & Myers, 2014) holotype; D= *J. (C.) iansa* (Petuch, 1979) holotype; E= *J. (C.) schirrmeisteri* Coltro, 2004 holotype; F= *Jaspidiconus ericmonnieri* Petuch & Myers, 2014 holotype; G= *J. henckesi* Coltro, 2004 holotype; H= *J. marinae* Petuch & Myers, 2014 holotype; I= *J. ogum* Petuch & Myers, 2014 holotype; J= *J. pomponeti* Petuch & Myers, 2014 holotype; K= *J. poremskii* Petuch & Myers, 2014 holotype; L= *J. pusillus* (Lamarck, 1810) lectotype.

*J. ogum* Petuch & Myers, 2014a  
(endemic to Aratuba, Itaparica Island,  
Brazil)

*J. pomponeti* Petuch & Myers, 2014b  
(endemic to Ribeira, Todos os Santos  
Bay, Brazil)

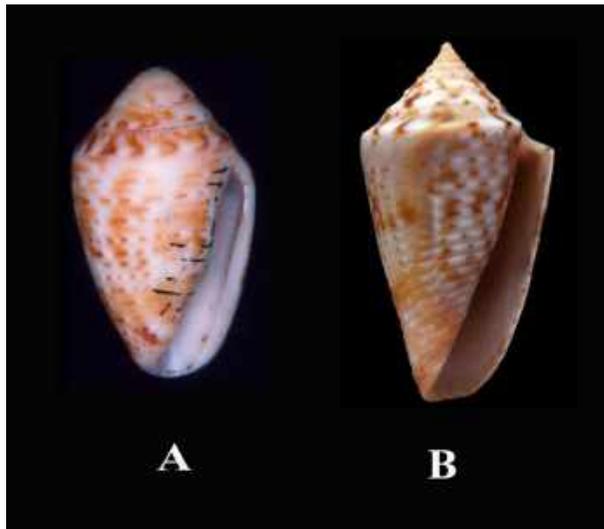
*J. poremskii* Petuch & Myers, 2014a  
(endemic to Bahia State, Brazil)

*J. pusillus* (Lamarck, 1810) (endemic  
to Brazilian Province)

### Paulinian Subprovince

*J. pusillus* (Lamarck, 1810) (endemic  
to Brazilian Province)

*J. simonei* Petuch & Myers, 2014b  
(endemic from Guarapari to central Rio  
de Janeiro State, Brazil)



**Figure 11. Paulinian Subprovince:** A= *Jaspidiconus pusillus* (Lamarck, 1810) lectotype; B= *J. simonei* Petuch & Myers, 2014 holotype.

### ANALYSIS

Although the conid genus *Africonus* in the Cape Verde archipelago has been determined to have undergone dramatic adaptive radiation, no such similar finding has previously been made concerning the conolithid genus *Jaspidiconus* in the Western Atlantic. *Africonus* evolved on a

number of small islands close together, some species seem to be restricted to a single bay of an island, and evolved in what has been called “explosive radiation” akin to a species flock (Duda & Rolan, 2005). At present, approximately 80 species of *Africonus* have been described. In comparison, the genus *Jaspidiconus* ranges from the Georgian Subprovince of the Carolinean Province, south to the Southern Paulinian Subprovince of the Brazilian Province - an area encompassing thousands of miles of coastline and hundreds of isolated islands, seamounts, coral cays, and coral reefs. *Jaspidiconus* which do not have a planktonic stage may be predisposed to greater genetic isolation due to their inability to transverse deep marine channels which separate many islands, leading to allopatric speciation. This hypothesis assumes that either (1) the ancestor of modern *Jaspidiconus* had planktonic larvae with wide dispersal abilities and that once in suitable habitats it evolved benthic development, or alternatively that (2) in the geological past sea levels varied as much as 100 meters higher or lower and the ancestral *Jaspidiconus* had a wide range across shallow seas connecting what are now distant islands. Allopatric speciation occurring across such a vast area, together with geographic isolation of *Jaspidiconus* species (both in terms of nautical distance and uninhabitable water depths which constitute reproductive barriers), and the fact that these Conoidean gastropods have benthic development accounts for the incredible biodiversity in the genus. The evolution of so many species of *Jaspidiconus* in these regions of the Western Atlantic is most likely a result of allopatric speciation and should certainly be less controversial than the similar adaptive radiation of *Africonus* which occurred in the shallow waters around the small archipelago of Cape Verde islands - a confirmed case of sympatric speciation; however at the scale of these

individuals, the mechanism is probably allopatric.

There have been very few radular studies (but see the comprehensive analysis of Tucker & Tenorio, 2009), and no morphometric analyses, conotoxin studies, or molecular studies of the various species hypotheses of *Jaspidiconus* (or many other genera of mollusks) to date, likely due to factors including availability of fresh specimens, funding, limited availability of technical experts and laboratory space. Many taxonomists today have been adding these methods into their analyses when comparing populations of mollusks and making a hypothesis by naming taxa, synonymizing taxa, or postulating the evolutionary relationships between species, much like scanning electron microscopes (SEM) were the latest scientific “tool” in the 1980s. This is not to say that mitochondrial RNA (“mRNA”) studies, or nuclear DNA studies are the best or the only approved method to determine species, however such studies are another new “tool” used by scientists in evaluating populations of organisms (Pulliandre, *et al.* 2014). Thoughts such as these constitute “molecular hubris” (Tucker personal communication). In fact, past mRNA molecular phylogenies on Conidae *s.s.* have not been conclusive, and more mRNA loci as well as nuclear DNA also should be included in such studies to obtain comprehensive results. A recent study found that mRNA expression is not always conserved across generations (as assumed in such studies) and is subject to gain and loss, as well as pervasive secondary loss, and these factors combined with significant sampling error collectively render mRNA based phylogeny analysis unreliable at best (Thompson, *et al.*, 2014). Molecular phylogenists proceed to collect mRNA (and occasionally one or two nuclear DNA loci) from dozens to hundreds of species, make unstated assumptions (including

but not limited to species hypotheses) and then after subjecting the data to a multivariate statistical cladistic or Bayesian analysis, some authors have made sweeping phylogenetic conclusions. Such studies based only on nucleic acid sequence data to the exclusion of other relevant properties therefore fail the requirement of total evidence (Fitzhugh, 2006) and constitute an inappropriate methodological hubris.

All species descriptions are a hypothesis. Therefore, whether the biodiversity seen in the Cape Verde Islands in the genus *Africonus*, and throughout the Caribbean in the genus *Jaspidiconus*, cannot be explained as hypothesized speciation events, and instead whether these “so called species” may more properly be called subspecies, phenotypic variation (or forms), or genetic variation within a species, remains to be determined by well reasoned studies that satisfy the scientific requirement of total evidence (Fitzhugh, 2005; Fitzhugh, 2006). There have been no such studies to date, therefore these species hypotheses should stand until proven to the contrary. Tried and true scientific methods of the last two hundred years such as morphology, anatomy, physiology, ecology, biogeography, and morphometric analysis are still the primary methods used by taxonomists to describe and compare species, genera and families, and to postulate about evolutionary relationships between groups. Future research on this fascinating group of rapidly evolving conoidean gastropods should include these primary methods as well as radular studies, conotoxin studies, and comprehensive molecular phylogeny studies to satisfy the requirement of total evidence and help understand the evolutionary relationships between these organisms, as is currently being done, albeit sporadically with a number of conoidean gastropods.

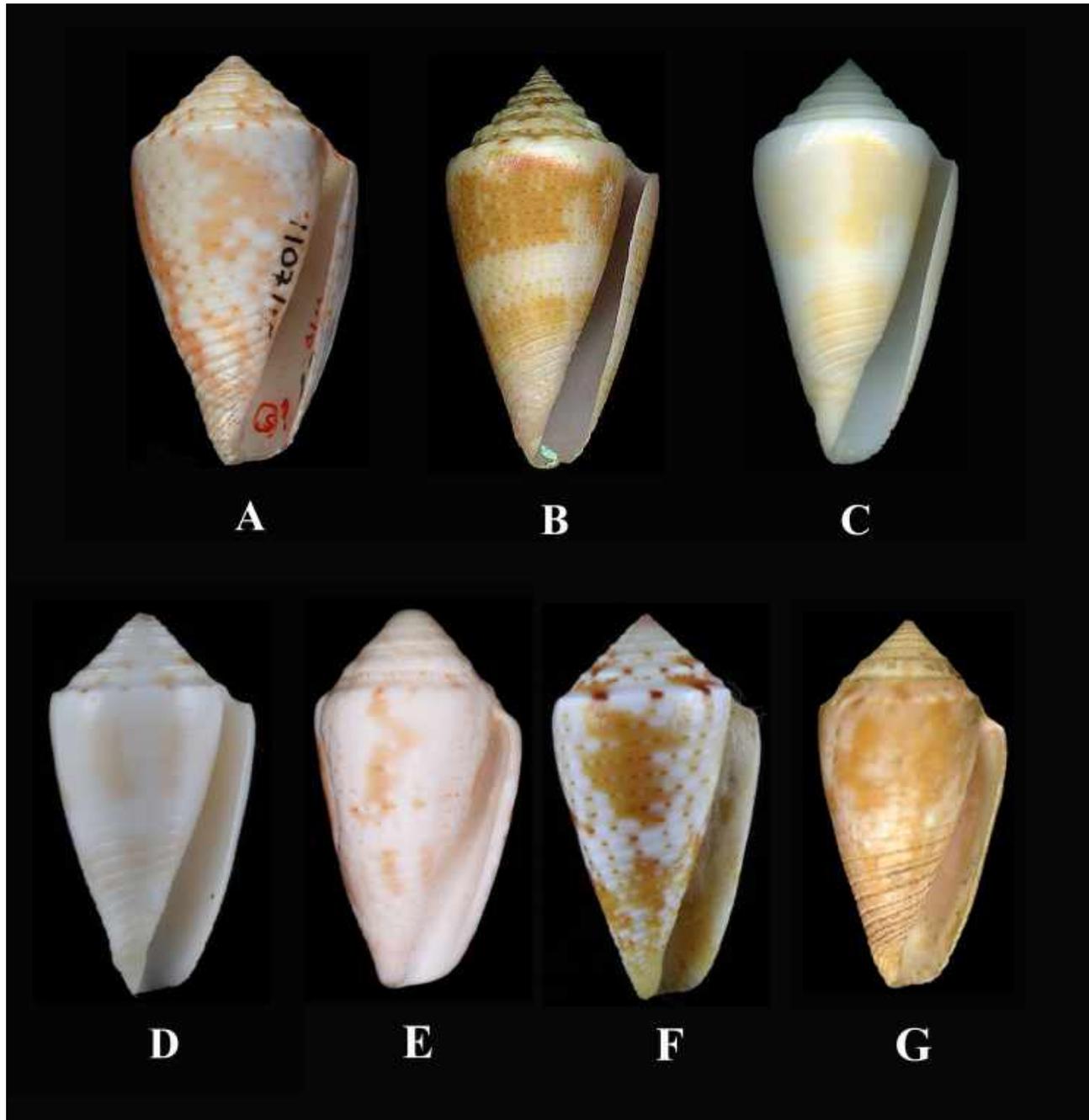
## ACKNOWLEDGEMENTS

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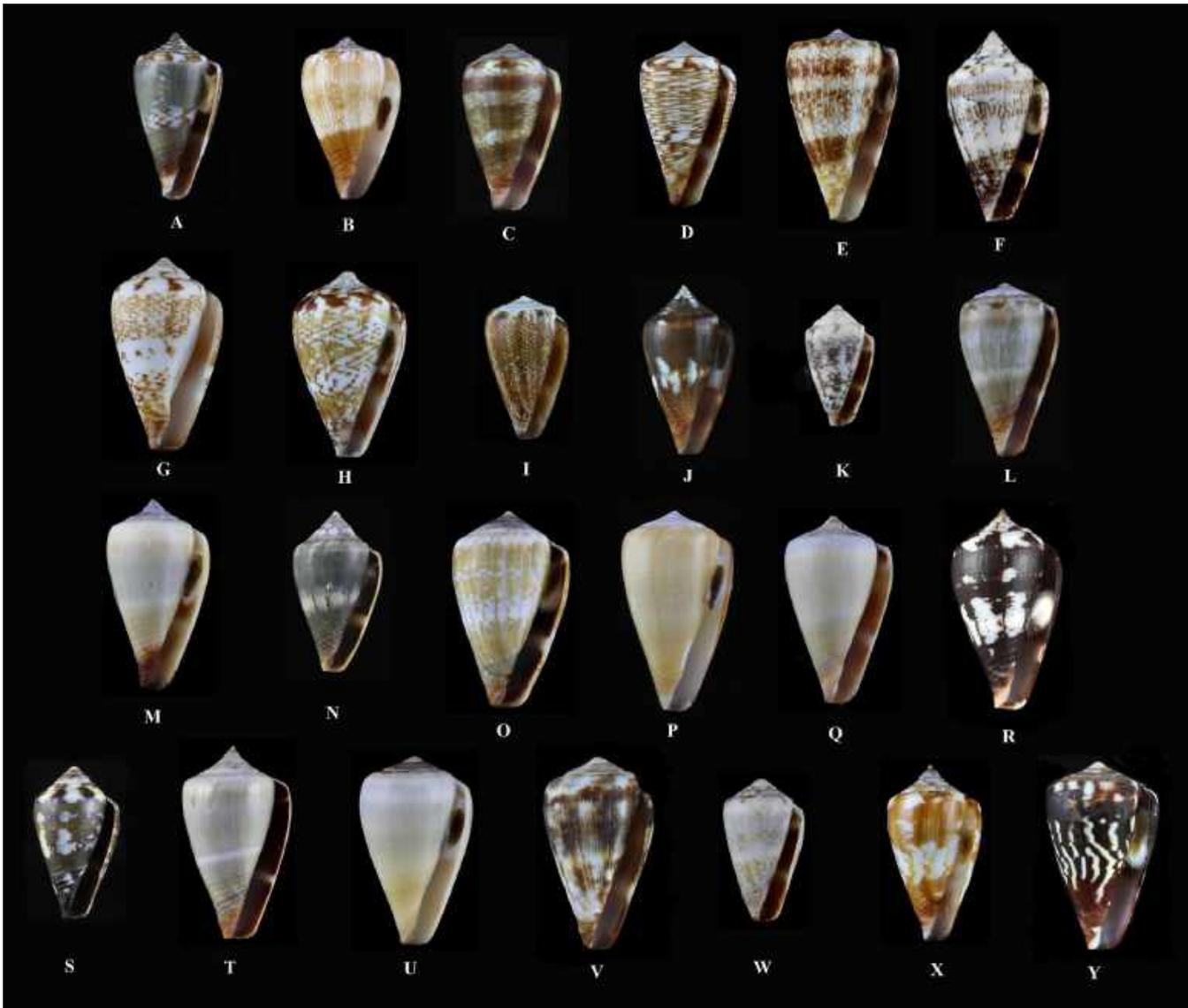
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- <sup>Δ</sup> **Note:** *Jaspidiconus alexandremonteiroi* Cossignani, 2014 is believed to be a subadult specimen of *Tukericonus ceruttii* (Cargile, 1997) by some experts, rather than a true *Jaspidiconus*. (Paul Kersten, António Monteiro, Edward Petuch, personal communication)

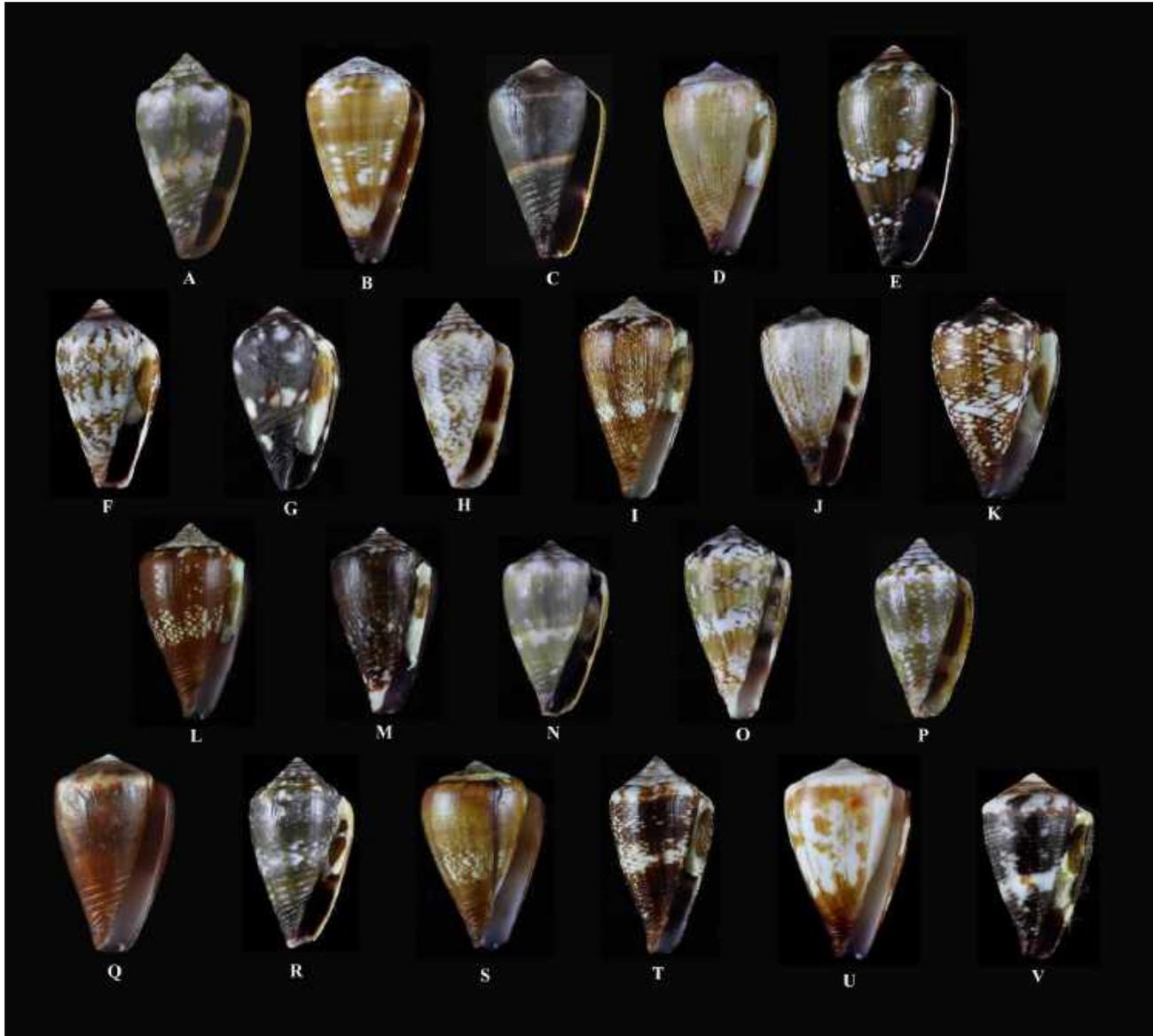


**Figure 12. *Jaspidiconus mindanus* subspecies and forms:** A= *Jaspidiconus mindanus* (Hwass in Bruguiere, 1792) lectotype; B= *J. ericmonnieri* Petuch & Myers, 2014 erroneously known for years as “*J. agassizii*” (see Figure 5a); C= *J. mindanus bermudensis* (Clench, 1942) holotype; D= *J. mindanus* from the David P. Berschauer Collection (collected by Peter Steelman, West Caicos); E= *J. mindanus karinae* (Nowell-Usticke, 1968) holotype; F= *J. mindanus karinae* (Nowell-Usticke, 1968) from the David P. Berschauer Collection (collected by Leo G. Ros, Malmok, Aruba); G= *J. mindanus lymani* (Clench, 1942) holotype.



**Figure 13. *Africonus* species: Figures A through Y**

**A** = *Africonus antoniomonteriroi* (Rolan, 1990), **B** = *Africonus borgesii* (Trovao, 1979), **C** = *Africonus cagarralensis* Cossignani, 2014, **D** = *Africonus crotchii* (Reeve, 1849), **E** = *Africonus cuneolus* (Reeve, 1843), **F** = *Africonus damottai* galeao (Rolan, 1996), **G** = *Africonus delanoyae* (Trovao, 1979), **H** = *Africonus derrubado* (Rolan & Fernandes, 1990), **I** = *Africonus evorai* (Monteiro & Fernandes, 1995), **J** = *Africonus fantasmalis* (Rolan, 1990), **K** = *Africonus felitae* (Rolan, 1990), **L** = *Africonus fontonae* (Rolan & Trovao, 1990), **M** = *Africonus fuscoflavus* (Rockel, Rolan & Monteiro, 1980), **N** = *Africonus infinitus* (Rolan, 1990), **O** = *Africonus irregularis* (Sowerby, 1858), **P** = *Africonus josephinae* (Rolan, 1980), **Q** = *Africonus luquei* (Rolan & Trovao, 1990), **R** = *Africonus maioensis* (Trovao, Rolan & Ilidio, 1990), **S** = *Africonus marcocastellazzii* Cossignani & Fiadeiro, 2014, **T** = *Africonus messiasi* (Rolan & Fernandes, 1990), **U** = *Africonus raulsilvai* (Rockel, Monteiro & Fernandes, 1998), **V** = *Africonus regonae* (Rolan & Trovao, 1990), **W** = *Africonus serranegrae* (Rolan, 1990), **X** = *Africonus swinnenii* Tenorio, Afonso, Cunha & Rolan, 2014, **Y** = *Africonus verdensis* (Trovao, 1979). [all specimens from the David P. Berschauer Collection]



**Figure 14. *Africonus* species: Figures A through V**

**A** = *Africonus antoniaensis* Cossignani & Fiadeiro, 2014, **B** = *Africonus antonioi* Cossignani, 2014, **C** = *Africonus cabraloi* Cossignani, 2014, **D** = *Africonus condei* Tenorio & Afonso, 2014, **E** = *Africonus cossignanii* Cossignani & Fiadiero, 2014, **F** = *Africonus crioulus* Tenorio & Afonso, 2014, **G** = *Africonus denizi* Afonso & Tenorio, 2011, **H** = *Africonus diegoi* Cossignani, 2014, **I** = *Africonus fiadeiroi* Tenorio, Afonso & Rolan, 2014, **J** = *Africonus gonsaloi* Tenorio & Afonso, 2014, **K** = *Africonus isabelarum* (Tenorio & Afonso, 2004), **L** = *Africonus joserochroi* Cossignani, 2014, **M** = *Africonus kersteni* (Tenorio, Afonso & Rolan, 2008), **N** = *Africonus melissae* (Tenorio, Afonso & Rolan, 2008), **O** = *Africonus mordeirae* (Rolan & Trovao, 1990), **P** = *Africonus morroensis* Cossignani & Fiadiero, 2014, **Q** = *Africonus sallaetae* Cossignani, 2014, **R** = *Africonus santaensis*, Tenorio & Afonso, 2014, **S** = *Africonus silviae* Cossignani, 2014, **T** = *Africonus vulcanus* (Tenorio & Afonso, 2004) **U** = *Africonus wandae* Cossignani, 2014, and **V** = *Africonus zinhoi* Cossignani, 2014. [all specimens from the David P. Berschauer Collection]