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Article *in* Journal of Molluscan Studies · May 2024

DOI: 10.1093/mollus/eyae019

José H. Leal
Bailey-Matthews National Shell Museum & Aquarium
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Gregory Herbert
University of South Florida
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Aaron Avery
University of South Florida
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Journal of
Molluscan Studies

The Malacological Society of London

Journal of Molluscan Studies (2024) **90**: eyae019. https://doi.org/10.1093/mollus/eyae019

Geometric morphometrics reveal that *Conus anabathrum* Crosse, 1865 (Neogastropoda: Conidae) should be an accepted species

José H. Leal[1], Gregory S. Herbert[2], William Fenzan[3], Aaron Avery[2] and Federico Márquez[4,5]

[1]*Bailey-Matthews National Shell Museum and Aquarium, 3075 Sanibel-Captiva Rd., Sanibel, FL 33957, USA;*
[2]*School of Geosciences, University of South Florida, 4202 E. Fowler Ave., Tampa, FL 33620, USA;*
[3]*401 Sinclair St., Norfolk, VA 23505 USA;*
[4]*Instituto de Biología de Organismos Marinos (IBIOMAR), Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Boulevard Brown 2915, Puerto Madryn, Chubut 9120, Argentina; and*
[5]*Departamento de Biología y Ambiente, Facultad de Ciencias Naturales, Universidad Nacional de la Patagonia San Juan Bosco, Boulevard Brown 3051, Puerto Madryn, Chubut 9120, Argentina*

Correspondence: J.H. Leal; e-mail: jleal@shellmuseum.org

urn:lsid:zoobank.org:pub:F7F022F1-08B7-4457-9E1A-C46446D112F0

(Received 24 January 2024; editorial decision 7 May 2024)

ABSTRACT

In 2022, the accepted name for a marine gastropod species from Florida until then known as *Conus anabathrum* Crosse, 1865, was replaced by *C. floridanus* Gabb, 1869. The main argument was that the type of *C. anabathrum*, a specimen with no type locality in the description, actually represents the eastern Pacific species *C. scalaris* Valenciennes, 1832. This allocation of the type of *C. anabathrum* to an eastern Pacific taxon was based on several factors, with shell shape as the main determinant. We demonstrate via geometric morphometrics that the type of *C. anabathrum* actually falls outside the morphospace of *C. scalaris*, belonging instead to the morphospace of the Floridian taxon. We also discuss other arguments presented to assign the type of *C. anabathrum* to the eastern Pacific species. These discussions and our geometric morphometric analytical results demonstrate that the type of *C. anabathrum* actually represents the Floridian species, and that *C. anabathrum* should be the accepted name.

INTRODUCTION

Conus anabathrum Crosse, 1865, is a medium-size cone snail commonly found in the eastern Gulf of Mexico, eastern Florida from about Jacksonville south, and the Yucatan Peninsula (Kohn, 2014). Berschauer (2022) proposed that the name *C. anabathrum*, accepted until recently, should be considered a junior synonym of eastern Pacific species *C. scalaris* Valenciennes, 1832. According to Berschauer (2022), the type of *C. anabathrum* (Natural History Museum, London, UK [NHMUK] 1979182, Fig. 1A), a specimen lacking locality data (Natural History Museum, 2021), represents *C. scalaris*, a species from the tropical eastern Pacific (Fig. 1B, holotype).

The nomenclature of *C. anabathrum* has endured some discussion. Crosse (1865) described *C. anabathrum* based on a single specimen in the Hugh Cuming collection. Crosse (1865) did not provide any locality information in the original description. Coomans, Moolenbeek & Wils (1980) examined the type of *C. anabathrum* and considered it to be conspecific with *C. floridanus* Gabb, 1869, a species from the western Atlantic. Coomans *et al.* (1980) designated “Coast of Florida” as the type locality of *C. anabathrum*. Vink (1985) agreed that the type of *C. anabathrum* represented *C. floridanus* and, based on the nomenclatural rule of priority, proposed the reinstatement of the binomen *C. anabathrum*. (The type of *C. anabathrum* is considered by the NHMUK to be a syntype, as Crosse (1865) did not fix a holotype in the original description—International Commission on Zoological Nomenclature [ICZN], 1999: Articles 72.1.1; 73.2; Recommendation 73G). Several years later, Cernohorsky (1987) advocated that “the re-introduction of this unused name [*Conus anabathrum*] for the well known [sic], common, living and Pliocene species *C. floridanus* poses a serious threat to nomenclatural stability.” Cernohorsky (1987) asked the ICZN to use its plenary powers “to suppress the name *anabathrum* Crosse, 1865, as published in the binomen *Conus anabathrum*, for the purposes of the Principle of Priority…” Harasewych & Petit (1988) opposed Cernohorsky’s (1987) request to the ICZN, maintaining that the binomen *C. anabathrum* “was validly proposed in a major malacological journal [the *Journal de Conchyliologie*], was adequately illustrated, and for which a holotype exists and has always been available for study in a museum noted for its care and curation of type material.” ICZN (1989) ruled not to conserve *C. floridanus* as a replacement name for *C. anabathrum*.

The issue at hand is not strictly nomenclatural, as it also involves species circumscriptions and their taxonomy. If, as proposed by

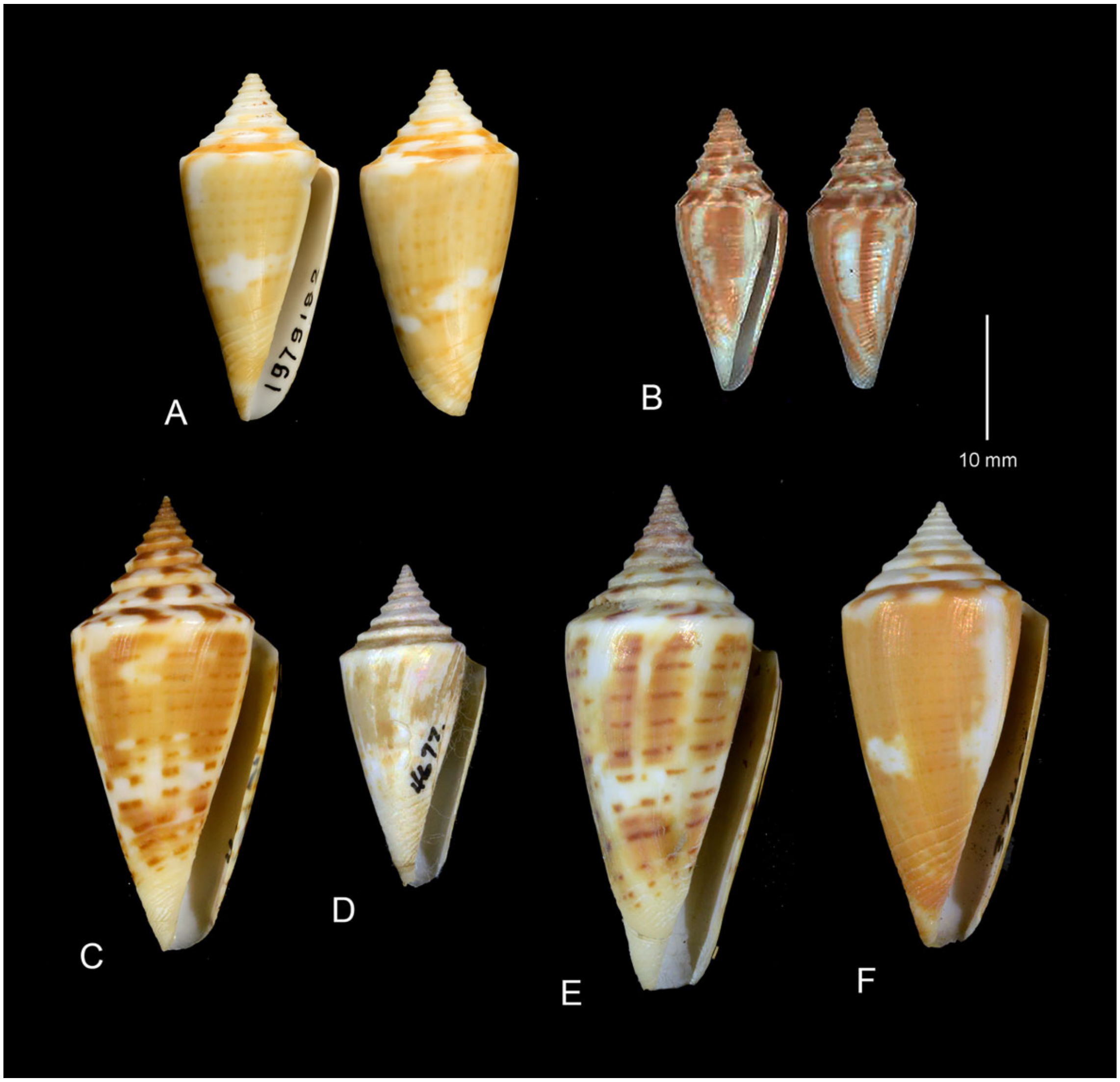

Figure 1. Specimens of *Conus* species referenced in this article. All images shown at the same scale. **A.** Type of *Conus anabathrum*, NHMUK 1979182, H = 29.1 mm (two views). **B.** Holotype of *C. scalaris*, MNHN-IM 2000–3313, H = 23.3 mm (two views). **C–F.** *C. anabathrum*. **C, D.** Examples with scalariform spire. **C.** BMSM 4683, Marco Island, FL, USA, H = 36.9 mm. **D.** BMSM 4677, Punta Rassa, Fort Myers, FL, USA, H = 25.5 mm. **E.** Example of a narrow shell, BMSM 21718, Sanibel, FL, USA, H = 42.3 mm; H/W = 2.31. **F.** Example with spire colour (compare with Fig. 1A), BMSM 37401, Pigeon Key, Florida Keys, H = 36.5 mm. Photo credits: **A**, Andreia Salvador, NHMUK; **B**, MNHN, C. Reyens.

Berschauer (2022), the name *C. anabathrum* proves to be a junior synonym of the eastern Pacific *C. scalaris*, the substitute (next available) name for the species would be, yet again, *C. floridanus*. Berschauer's article was published in April 2022, and the name change from *C. anabath*rum to *C. floridanus* was quickly implemented in May of that year by MolluscaBase (MolluscaBase eds., 2023) and WoRMS (WoRMS Editorial Board, 2023).

In this article, we reopen the discussion started by Berschauer (2022), questioning some of his statements regarding the type of *C. anabathrum* and how this shell relates to the associated western Atlantic and eastern Pacific species. We also used geometric morphometrics methods to check the placement of general shape attributes for the types of *C. anabathrum* and *C. scalaris* and how they compare to shells of these two species with reliable locality data. Geometric morphometrics analytical techniques and associated landmark analyses of data collected as bidimensional coordinates allow for direct quantification of variation in biological shape (Cruz, Pante & Rohlf, 2012). Such techniques have been successfully employed in taxonomic studies of the Conidae (Cruz *et al.*, 2012; Tenorio, Tucker & Chaney, 2012). The results of the present study do not directly relate to nomenclatural stability or priority, but to the accurate identity of the type of *C. anabathrum* as representative of the western Atlantic or eastern Pacific species.

MATERIAL AND METHODS

Shell photography for geometric morphometrics

Shells were photographed on copystands using either a Nikon D800 camera with a Micro-Nikkor 60-mm macro lens or a Canon DSLR with Canon MP-E 65 mm or Zeiss Makroplanar 100 mm. Images were taken with the shell aperture up and the shell axis of each specimen parallel to the image plane, following, for consistency in the assignment of landmarks, the standardization parameters provided by Callomon (2019). Shell measurements were taken directly from each image, via a scale ruler in mm placed near each shell, with the scale ruler plane parallel to the shell axis. Additionally, we incorporated images and dimensions of the types of *C. anabathrum* (Fig. 1A, NHMUK 1979182, image courtesy Andreia Salvador, NHMUK; see Natural History Museum, 2021) and of *C. scalaris* (Fig. 1B, Muséum national d'Histoire naturelle [MNHN-IM] 2000–3313; see MNHN, 2023). Images for comparisons are depicted in Figures 1C–F. All images were originally acquired following the standard orientation for photography of cone snails as adopted in this study.

Selection of specimens for geometric morphometrics

Given the serious confusion and misidentifications involving the identity of *C. scalaris* and other species in the so-called "*C. gradatus* complex" (Lauer, 1995), we decided to restrict the photography of specimens of *C. scalaris* to two selected collections. The Santa Barbara Museum of Natural History (SBMNH) and William Fenzan Collection (WFC) collections of *C. scalaris* have been curated taking into account the narrower definition of the species as described by Lauer (1995). Fourteen shells of *C. scalaris* from the SBMNH and 12 shells from WFC were photographed. *Conus anabathrum* was represented by 29 shells from the Bailey-Matthews National Shell Museum (BMSM). We strived to cover as much of the geographic range of each species; the Supplementary Material includes a list of localities and geolocation for the shells examined in this study. We included three specimens in the analysis that may be considered by some to be "*C. burryae*," as we wanted to cover the broader *C. anabathrum* phenotype. There is debate whether there is a single variable species with regional ecophenotypes, regional species that are distinct but not at the level of full species, or two recently diverged species (Kohn, 2014: 312). For instance, Kohn, 2014 (p. 318) considered the holotype of *C. burryae* to be well within the morphological variation of *C. anabathrum*. As an example, we ran the same analyses excluding samples that could be assigned to "*C. burryae*" by some, but the exclusion of those three shells did not significantly affect the analyses presented herein.

Since sexual dimorphism expressed as differences in shell proportions between males and females has been described for at least two species of cone snails, *C. mappa* [Lightfoot], 1786, and *C. centurio* Born, 1778 (Percharde, 1984), we would like to address this issue and how we dealt with it. We used dry museum samples for which the sex of the animal was unknown. We are not aware of sexual dimorphism in the studied species. If there is sexual dimorphism, we chose specimens to capture a broad range of shapes for both the Florida and eastern Pacific species in a way that would not bias the sample toward either sex. Similarly, if sex dimorphism is also expressed as size differences, our range of shell sizes from 24.6 to 54.3 mm (*C. anabathrum*) and 19.9 to 51.8 mm (*C. scalaris*) shell height should represent relatively unbiased metrics. These size ranges also encompass the sizes of types, which are small. In anticipation of the results and discussion in this report, we are referring to Florida shells throughout this article as *C. anabathrum*.

Digitization and landmarking

Images were compiled and digitized, and randomly ordered using TpsUtil (Rohlf, 2017a) and TpsDig2 (Rohlf, 2017b). Ten landmarks (fixed point defined as a discrete biological form) and 15 semi-landmarks (a particular type of landmark used to discretize variation in contour) were placed on the body whorl and spire (Fig. 2), but avoiding the lip (see Smith & Hendricks, 2013). The landmark and semi-landmark configuration was employed following the methodology of Cruz *et al.* (2012) and Márquez, Primost & Bigatti (2017). Semi-landmarks are configured to describe as much of the outline shape variation as possible (Márquez *et al.*, 2017). Semi-landmarks are identified as nonhomologous points and are allowed to 'slide' between landmarks as dictated by shape change (Bookstein, 1997). A mathematical iterative algorithm that minimizes the TPS function's bending energy was used to homologize semi-landmarks in the software TpsRelw (Rohlf, 2017c). Landmarks and semi-landmarks were applied in the same order for every shell image by the same researcher.

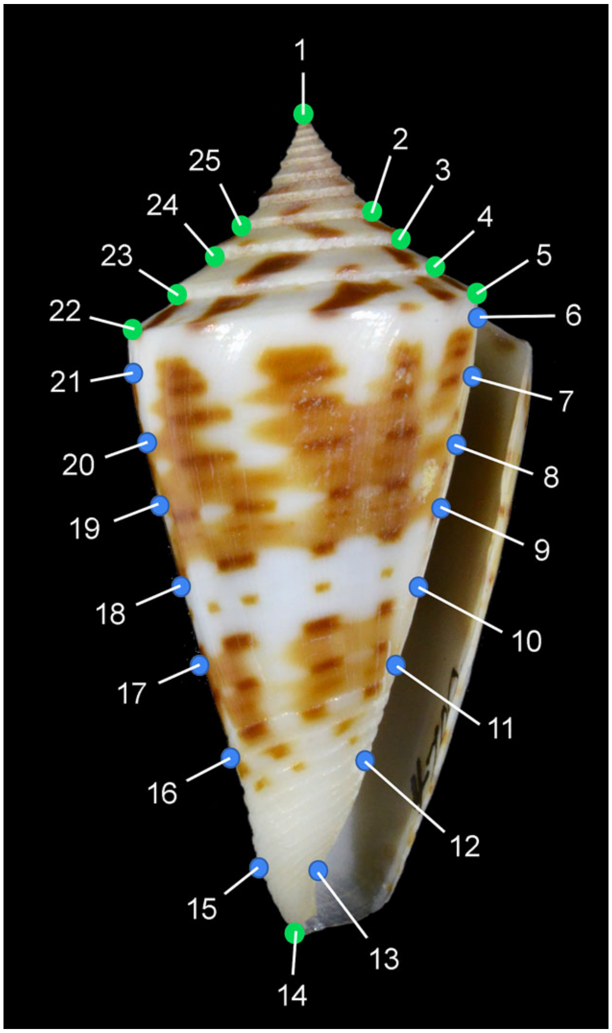

Figure 2. *Conus anabathrum* shell (BMSM 4700), H = 39.9 mm, showing positions of 10 landmarks and 15 semi-landmarks. Landmarks: 1, apex; 2–4, suture between major whorls on right; 5, shoulder of last whorl on right; 6, junction between end of suture and apertural lip; 14, anterior tip of columella; 22, shoulder of last whorl on left; 23–25, suture between major whorls on left. Semi-landmarks: 6–13, between landmarks 5 and 14; 15–21, between landmarks 14 and 22.

Geometric morphometric analysis

Procrustes alignment, which eliminates the effect of rotations, translation and scale, was performed using the software TpsRelw (Rohlf, 2017c). The pure shape information was preserved as aligned specimens and exported to MorphoJ software (Klingenberg, 2011) for the statistical shape analysis. The centroid size (CS) was used as a proxy for shell size. The CS was calculated as the square root of the sum of the squared distances from the landmarks and semi-landmarks to the centroid defined by those landmarks and semi-landmarks (Zelditch *et al.*, 2004). To test for allometry (change in shape with increase in size), we applied a pooled-within-species multivariate regression analysis between shape scores (aligned

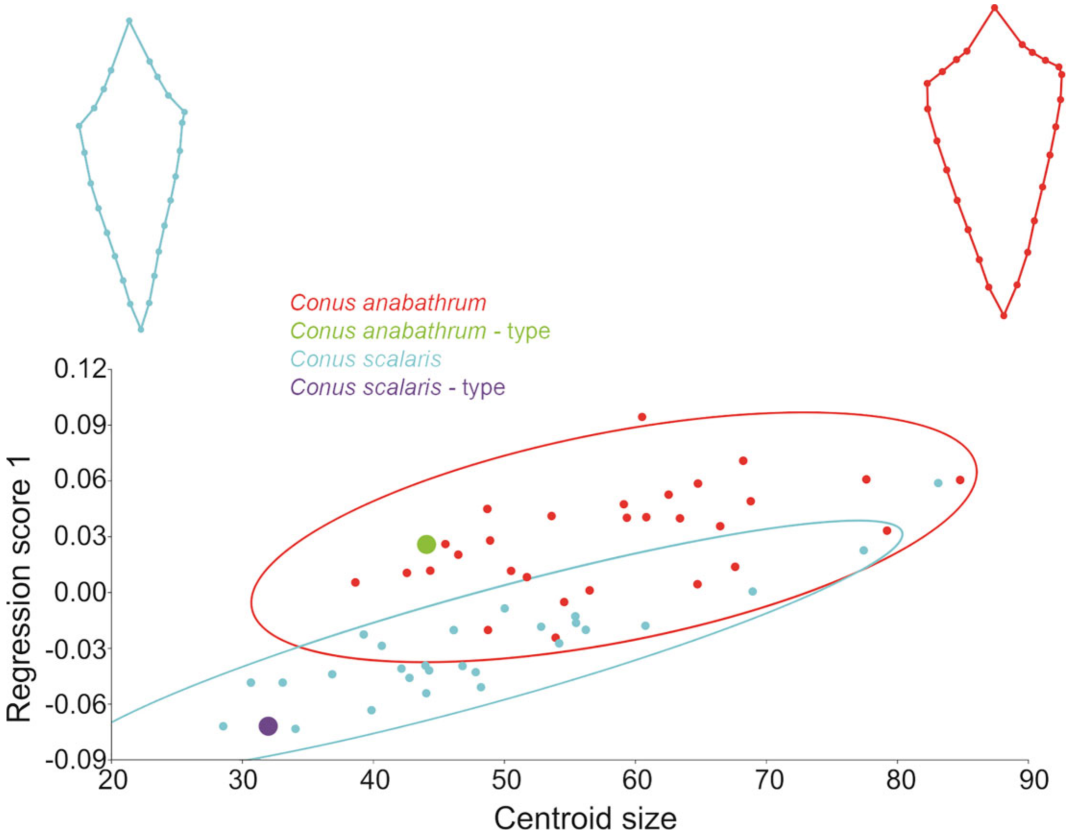

Figure 3. Allometric growth of the shell of *Conus anabathrum* and *C. scalaris*, and the relative positions of their respective types. Wireframe graphs show shell shape changes between the smallest (left) and largest (right) individuals from the two species analysed in this study. Ellipses delimit a 95% predicted probability for specimens of *C. anabathrum* and *C. scalaris* of falling within their boundaries.

Procrustes coordinates, dependent variable) and size (CS, independent variable) (Bookstein, 1997; Monteiro, 1999). Variation of shell shape explained by allometry was quantified as the percentage of the total shape variation accounted for by the regression model (Klingenberg & McIntyre, 1998). Independence between shape and size variables was assessed with a permutation test (10,000 rounds). Next, the principal component analysis (PCA) from a variance-covariance matrix, generated using a shape coordinate dataset (aligned individuals), was calculated to display the major traits of shell shape variation. The principal component (PC) scores of the individuals were used to calculate a discriminant analysis (DA) to capture the shape components that maximized the separation between the Floridian and eastern Pacific species, and to calculate the discriminant function. This previously defined discriminant function was used to assign the types of *C. anabathrum* and *C. scalaris*, without group information, to the Floridian and eastern Pacific species. The DA was performed using Infostat statistical software (Di Rienzo *et al.*, 2020). The same statistical analyses were used by Van der Molen *et al.* (2013) and Trovant *et al.* (2018) to assign extant and fossil individuals to morphospecies.

Acronyms and abbreviations

BMSM	Bailey-Matthews National Shell Museum, Sanibel, FL, USA
H	shell height
H/W	ratio shell height/shell width
SBMNH	Santa Barbara Museum of Natural History, Santa Barbara, CA, USA
MNHN-IM	Muséum national d'Histoire naturelle, Paris, France, Molluscs
NHMUK	The Natural History Museum, London, UK
W	shell width
WFC	William Fenzan Collection, Norfolk, VA, USA

RESULTS

Based on multivariate regression between shape and centroid-size pooled within-species, 27. 3% ($P < 0.0001$) of shape variation was predicted by size (Fig. 3). Regression residuals were then used as new size-unrelated shell shape variables in subsequent statistical analysis. In the PCA, the first two PCs explained 82.6% of the total variation (Fig. 4), while the other PCs accounted for <5% of the total variance and were ignored (Zelditch *et al.*, 2004). In the resulting morphospace, the PC1 axis represents the shell shape variation between species. Geometric interpretation of the positive values of PC1 was related to the lateral compression and taller spire, while the negative values were related to the opposite shape values. The positive values represent the individuals of *Conus scalaris*, while the negative ones are associated with *C. anabathrum* (Fig. 4). The mean shell shape of *C. scalaris* is slender, more elongated than that of *C. anabathrum* (T^2 Hotelling = 2501.8, $P < 0.001$; Fig. 5). The types of *C. anabathrum* and *C. scalaris* were allocated (Fig. 4) to the respective species using the discriminant function.

DISCUSSION

Our geometric morphometric comparison of shell shapes demonstrates that (1) the main difference in shape between western

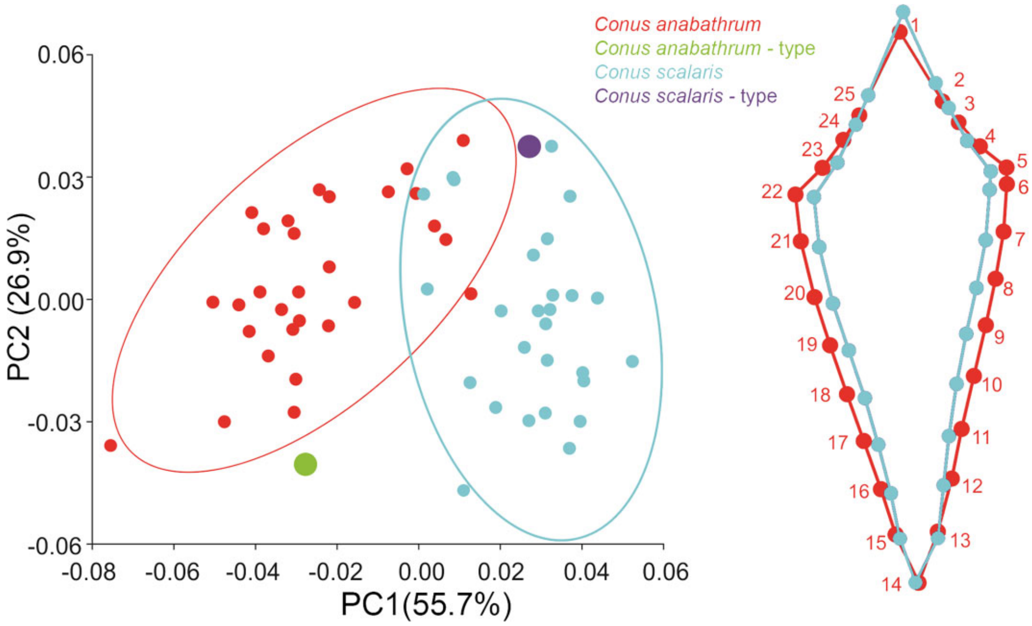

Figure 4. The principal component analysis shows the morphospaces defined by the two species and the relative positions of the types of both species. The wireframes represent displacement vectors from the consensus shape to the positive extreme shape using a scale factor of 0.1.

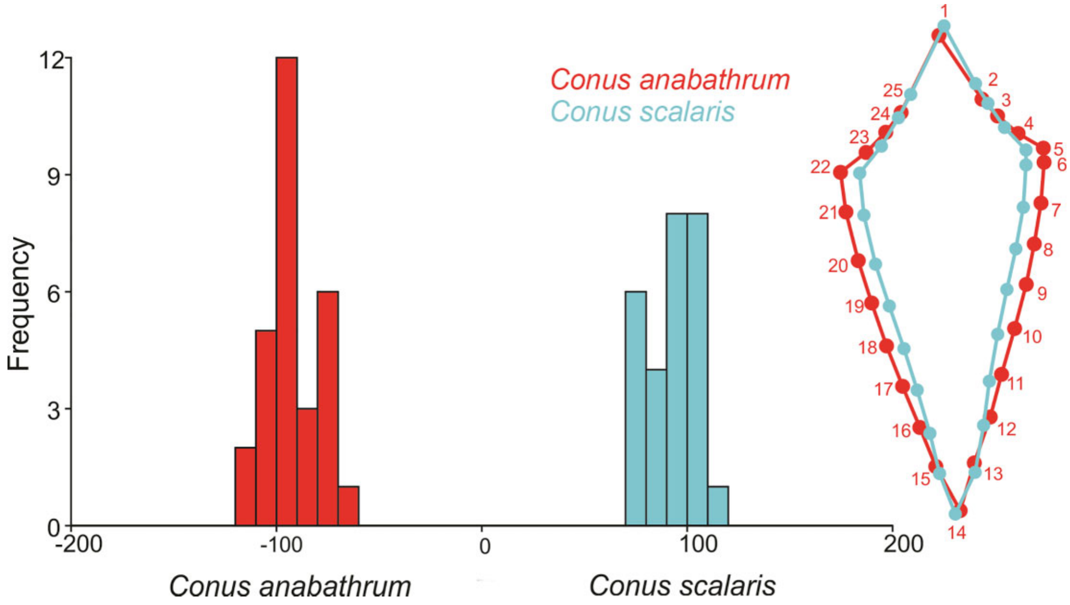

Figure 5. Discriminant analysis of the shell shape differences between species. Frequencies of the discriminant scores are shown using histogram bars. The mean shapes of *Conus anabathrum* and *C. scalaris* are visualized using wireframes.

Atlantic shells assigned to *Conus anabathrum* and eastern Pacific shells identified as *C. scalaris* is the greater lateral compression of the latter species, and (2) the shell shape of the type of *C. anabathrum* falls definitively within the morphospace of the western Atlantic species but significantly outside the morphospace of *C. scalaris* when shape variation related to size is taken into account. Thus, our results contradict Berschauer's (2022) assertion that *C. anabathrum* is an eastern Pacific taxon and a junior synonym of *C. scalaris*. Rather, shell shape supports prior opinions that the *C. anabathrum* type is a western Atlantic species conspecific with *C. floridanus* as proposed more than four decades ago by Coomans *et al.* (1980) and later accepted by Vink (1985). In addition, the small shape differences within the broader Floridian *C. anabathrum* phenotype obviously did not affect the geometrical morphometrics results because the Pacific and Floridian groups are clearly distinct and the type of *C. anabathrum* clusters unambiguously outside of the Pacific group and within the Floridian group.

Although quantitative analysis of shell shape is the most rigorous approach to resolve the identity of the type of *C. anabathrum*, we must also address Berschauer's (2022) arguments that *C. anabathrum* is an eastern Pacific species. First, Berschauer (2022) claimed that Hugh Cuming, owner of the type of *C. anabathrum*, collected only in the eastern Pacific and did not have access to shells from the western Atlantic. To support this statement, Berschauer (2022) quoted

Dance (1980), who described in detail Cuming's extensive travels in the Pacific. However, Dance (1980) also discussed how Cuming, when replenishing his stock of shells for sale, kept "adding more and more specimens to his collection by exchange and purchase" (Dance, 1980: 491), including attending auctions where shells from the western Atlantic would have been available. Cuming also "induced other traveller-naturalists to collect specimens for him in far away places, notably in the tropics." In particular, Dance (1980: 491) mentioned collector Philip Henry Gosse and how Cuming established contact with him prior to Gosse's trip to Jamaica, again establishing Cuming's connection to a source of western Atlantic shells. In Gosse's biography, his son Edmund (Gosse, 1890: 118–120) further recalled that his father visited and collected in the USA and travelled on a boat through the Gulf of Mexico, with stops in the Florida Keys and Alabama. Most importantly, Dance (1980: 494) observed that "In 1851 [Cuming] even ventured as far as the United States to make the acquaintance of conchologists there." Crosse (1865) also named *Conasprella anaglyptica* (as *Conus anaglypticus*), another western Atlantic species that also originated from the Cuming collection. Consequently, the fact that the type of *C. anabathrum* originated from the Hugh Cuming collection cannot be used to allocate that shell exclusively to the eastern Pacific.

Next, Berschauer argued that the scalariform spire of the *C. anabathrum* type is "reminiscent of a number of eastern Pacific *Gradiconus* species," while Florida shells have "a fairly smooth slightly concave spire" (Berschauer, 2022: 44). However, a scalariform spire is also present, to varying degrees, in shells of the western Atlantic taxon (see Figs 1C, D); see also Kohn (2014: 315, pl. 85, fig 25).

As a third argument, Berschauer (2022) claimed that the relatively narrow shape of the *C. anabathrum* type is more similar to the Pacific *C. scalaris* than to the broader Floridian cone species. However, Berschauer did not provide any quantitative evidence to support this assertion, while our quantitative analysis conclusively shows the shell shape of the *C. anabathrum* type to be typical of shells of the western Atlantic taxon and to fall outside the range of variation of the eastern Pacific *C. scalaris*. The type of *C. anabathrum* is just 29.1 mm. Rosenberg (2009) lists the maximum size of the Floridian cone species as 51 mm. That means that the *C. anabathrum* type could be narrow because it is a juvenile shell. In our analysis, smaller shells of both species are predictably narrower.

Berschauer's (2022) last claim is that the spire of the type of *C. anabathrum* is completely orange and closer to the orange spire of *C. scalaris* than to the whiter spires of the Floridian shells: "[in *C. scalaris*] the whorl tops are almost completely orange with occasional small white blotches" and "[in *C. anabathrum*] the whorl tops are white with faint orange flammules." However, the spire of the type of *C. anabathrum* is not completely orange but has a whitish background with orangish markings, as do so many Floridian specimens. Although there is orange on the shoulders of the three last whorls of the type of *C. anabathrum*, the whorls preceding them are mostly white. For example, compare Figure 1A (type of *C. anabathrum*) with Figure 1F. Thus, spire colour also does not rule out a Florida origin for the *C. anabathrum* type.

ACKNOWLEDGEMENTS

We are grateful to Daniel Geiger (SBMNH) for taking photos of the specimens of *Conus scalaris* from the SBMNH used in this study. Henry Chaney (SBMNH) confirmed the identity of those specimens. Andreia Salvador (NHMUK) sent high-resolution images of and provided information about the type of *C. anabathrum*. Two anonymous reviewers provided comments and criticisms that refined the content and clarity of the manuscript. This study was funded in part by the National Science Foundation (grant award DBI-2001528) under the project "Digitization TCN: Mobilizing Millions of Mollusks of the Eastern Seaboard" to J.H.L.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Journal of Molluscan Studies* online.

DATA AVAILABILITY

Access to taxonomic and collection-event data for the molluscan shells mentioned in this study is available through the BMSM and SBMNH's institutional mollusk collection databases. The collection numbers and data to specimens cited in this publication are available as Supplementary Material.

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