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Opening Pandora's box: diagnostics characters for the confuse taxonomy of the Brazilian *Cardiomya* (Bivalvia: Cuspidariidae)

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Abstract

The unsolved systematics of the genus *Cardiomya* has led to a sequence of astonishing identification mistakes. This scenario is a result of the rarity of specimens and, more importantly, the lack of knowledge about which characters are relevant to the genus taxonomy. In this study, we developed a method based on standard linear discriminant analysis to identify the smallest number of morphological characters that efficiently distinguish individuals at the species level of Brazilian *Cardiomya*. Starting from 29 morphometric measurements obtained from photographed *Cardiomya* shells, we were able to identify only five characters: the dorsal inflection of the rostrum, the distance from the posterior most rib end to the umbonal posterior margin and the distance from the central point of the valve to the anterior margin at 45°, 15° and −30° angles. Surprisingly, all these characters are related to the shell outline and not the ornamentation, which is a remarkable character in *Cardiomya*. We performed a one-way ANOVA with post-hoc Tukey HSD test specifically using the total number of ribs to verify its discriminant power in species identification. Our analysis demonstrated that the number of ribs does not show a significant difference between the analysed species.

Introduction

Although easily distinguished from other confamilial genera mainly due to its radial ornamentation, species delimitation within *Cardiomya* is far from resolved. The length of the rostrum and the number of radial ribs are traditionally suggested as diagnostic characters of *Cardiomya* species (d'Orbigny, 1841–1853; Jeffreys, 1876; Dall, 1881; Allen and Morgan, 1981; Barroso *et al*., 2016; Machado *et al*., 2017; Oliveira *et al*., 2017; de Lima *et al*., 2020), but the polymorphic variation of these characters has long caused taxonomic ambiguities and frequent misidentifications, rising doubts on the value of their use for the systematics of the genus. Not unexpectedly, from the 72 described species, about 20 correspond to invalid names (MolluscaBase eds., 2022).

Recent taxonomic revisions raised an astonishing sequence of mistakes, exemplifying the yet unsatisfactory resolution of the *Cardiomya* systematics. For instance: *Cardiomya perrostrata* (Dall, 1881) has been reported to Brazilian waters for about 50 years, but the records before Oliveira *et al*. (2017) have been proven to be based on misidentifications. Similarly, after the examination of the specimens previously identified as *Cardiomya cleryana* d'Orbigny, 1842 deposited in Brazilian collections, de Lima *et al*. (2020) revealed a mix of distinct misidentified taxa, including four undescribed morphotypes (one of them described as *Cardiomya minerva* de Lima, Oliveira and Absalão, 2020), and one new occurrence (i.e. *Cardiomya striolata* (Locard, 1897)).

Both *C. perrostrata* and *C. cleryana* are the two most extensively studied and most abundant species in Brazil. When we extrapolate this scenario of misidentifications to the less abundant species, the implications are even more serious. The key factors that contribute to this scenario are the rarity of the specimens, the difficulty of collecting new samples and the lack of knowledge about which characters are relevant to the taxonomy of the genus *Cardiomya* (Oliveira *et al*., 2017).

Six described *Cardiomya* species have been reported to Brazilian waters (de Lima *et al*., 2020): *Cardiomya cleryana* (d'Orbigny, 1842); *Cardiomya ornatissima* (d'Orbigny, 1853); *Cardiomya striata* (Jeffreys, 1876); *Cardiomya perrostrata* (Dall, 1881); *Cardiomya striolata* (Locard, 1897) and *Cardiomya minerva* de Lima, Oliveira and Absalão, 2020. In the present study, we investigate morphometric variation within *Cardiomya* species looking for the smallest number of morphological characters capable of efficiently distinguishing individuals at species level in order to designate their respective variables as the most informative one for this group.

Material and methods

Examined material

The specimens examined in this study are deposited in the following institutions: CMPHRM-A = Coleção Malacológica Professor Henry Ramos Matthews, Fortaleza, Brazil; IBUFRJ = Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil; MACN = Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Buenos Aires, Argentina; MCZ = Museum of Comparative Zoology, Cambridge, UK; MNHN = Muséum national d'histoire naturelle, Paris, France; MNHNM = Museo Nacional de Historia Natural, Montevideo, Uruguay; MNRJ = Mollusca Collection of the Museu Nacional / UFRJ, Rio de Janeiro, Brazil; MORG = Museu Oceanográfico 'Professor Eliézer de Carvalho Rios', Universidade Federal do Rio Grande, Rio Grande, Brazil; MZUSP = Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil; NHMUK = Natural History Museum, London, UK; RMNH.MOL = Naturalis Biodiversity Center, Leiden, Netherlands; USNM = Smithsonian Institution, National Museum of Natural History, Washington, USA; ZMUC = Zoological Museum – University of Copenhagen, Copenhagen, Denmark; ZUEC-BIV = Coleção de Bivalves do Museu de Zoologia da Universidade Estadual de Campinas, Campinas, Brazil. All types of the analysed species were included in the present study, the list of all lots used is available in Supplementary Table S1.

Variables

For the statistical data analysis, the selected specimens were photographed in external view and the morphometric measurements were performed using the ImageJ open-source software (Rasband, 1997–2018). In total, 29 morphometric measurements were selected to extract variation in the shell outline and ornamentation (Figure 1), including 24 linear distance measurements, three angular measurements and two meristic data. The variables are abbreviated as follows:

Linear measurements parallel to antero-posterior axis: total length (1); anterior length, from posteriormost rib base to anteriormost shell margin (2); rostrum length, from posteriormost rib base to posterior limit of the rostral margin (3).

Linear measurements parallel to dorso-ventral axis: total height (4); rostrum height (5); rostral base height, from the posteriormost rib distal end to the rostrum dorsal margin (6); dorsal inflection of the rostrum (7), a horizontal line is drawn flush with the umbones, and from it, a vertical line is extended to this line until the most inflected part of the rostrum.

Other linear measurements: rostral distal height, the distance of the most distal limit between dorsal and ventral rostral margin (8); distance from the posteriormost rib end to the posterior limit of the rostral margin (9), to the ventral rostral tip (10) and to the umbonal posterior margin (11); width of the three posteriormost ribs (12, 13, 14); distance between these ribs (15, 16); ventral inflection of rostrum (17); distance from the central point of the valve to the anterior margin (21) in a 45° angle (24), 30° angle (23), 15° angle (22), −15° angle (20), −30° angle (19) and −45° angle (18), the maximum height and maximum length are measured, and the central point between these two measurements is marked.

Angular measurements: anterior (25) and posterior (26) umbonal angle; rostrum inflection angle, defined by the angle between the umbonal and dorsal rostral tips (27).

Meristic data: total number of ribs and number of primary ribs as defined in Carter *et al*., 2012.

Data analysis

The examined material was first identified at species level by comparing with the type material and following d'Orbigny (1841–1853); Jeffreys (1876); Dall (1881); Locard (1897); de Lima *et al.* (2020). Only unequivocally identified specimens were included. Juveniles or individuals without fully formed rostrum and indistinguishable primary and secondary ribs were not considered. From the six Brazilian species, only *Cardiomya minerva* could not be included in the present study due to the scarcity of the material. This species was described based on one shell only, and since its original description no new specimens were found. To avoid potential bias caused by the inequivalve shell in *Cardiomya*, the valves were separated in two sets according to their side (i.e. left or right) and the analysis was divided into three stages: (1) only left valves, being 62 valves of *C. cleryana*, 48 valves of *C. perrostrata*, 23 valves of *C. ornatissima*, 16 valves of *C. striolata* and 7 valves of *C. striata*, totalling 156 valves; (2) only right valves, being 7 valves of *C. cleryana*, 37 valves of *C. perrostrata*, 15 valves of *C. ornatissima* and 14 valves of *C. striolata*, totalling 73 valves; (3) both left and right unarticulated valves, being 69 valves of *C. cleryana*, 85 valves of *C. perrostrata*, 38 valves of *C. ornatissima*, 30 valves of *C. striolata* and 8 valves of *C. striata*, totalling 230 valves. Within this dataset, there are 4 shells of *C. cleryana*, 16 shells of *C. perrostrata*, 4 shells

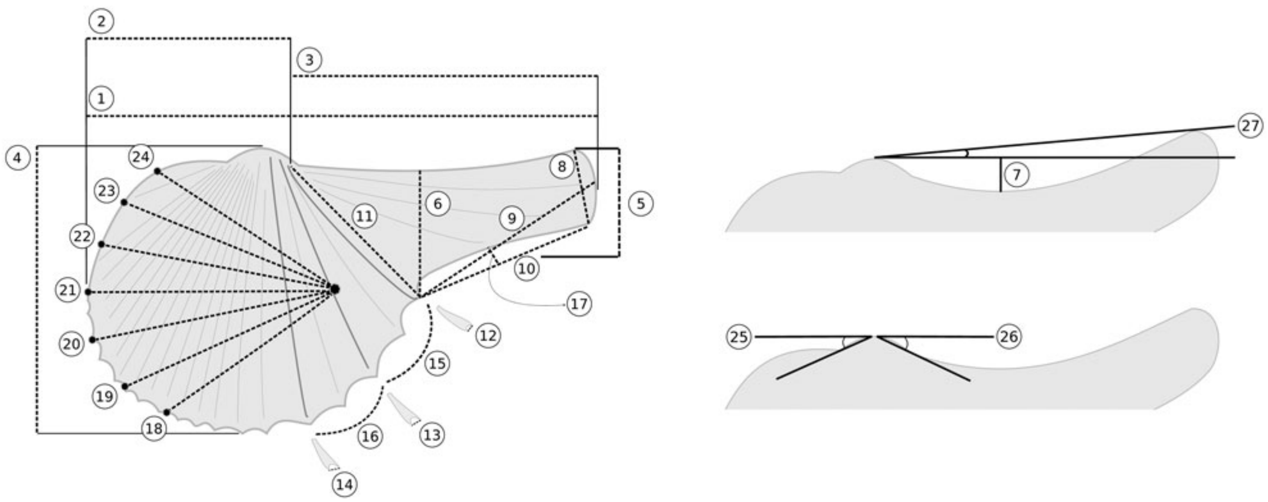

Figure 1. Pictographic glossary displaying measured variables.

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of *C. ornatissima*, 9 shells of *C. striolata* and 1 shell of *C. striata*, totalling 34 integer individuals.

All 29 variables were analysed using a standard multiclass linear discriminant analysis (LDA) (Fisher, 1936; Rao, 1948). Aiming to not discard at first inequivalve variables, the selection of the most informative ones were done using only one valve. Following this procedure, there were no preferential variables and it was possible to test later in the analysis if the variables selected could be extrapolated to the opposed valve. As the left valves were the most abundant, they were chosen as a base to determine the most informative variables. The left valve dataset was divided into two, a training dataset containing 50% of the original data obtained via a stratified random sampling that took into account the uneven number of specimens in each class and a test dataset with the remaining data. The algorithm to determine the most informative variables consists of applying the LDA in the training dataset with all possible combinations of three morphometric variables and selecting the one with lowest Bayesian information criterion (BIC) relative to the others (Schwarz, 1978). One by one, new variables were added to the best set of three variables to check if there was an improvement on the criteria. This procedure ensures a feasible computing time for the method. Having determined the most informative variables, the training dataset is used to define three discriminant functions (DF) that will classify a specimen in one of the possible species classes. The test dataset evaluates if the DF defined in the training process can be extrapolated for the species population by measuring the fraction of specimens correctly labelled in an unseen dataset, i.e. specimens not used in the original training phase.

A Wilks-Lambda test was used to evaluate the statistical significance of the DF classification. For the analysis, a specimen was considered an outlier if one of the most informative variable measurements were outside the usual interquartile rule: the first quartile minus 1.5 times the interquartile range and the third quartile plus 1.5 times the interquartile range. The code implementing this analysis was written in Python using the open-source libraries Pandas (McKinney, 2010), Numpy (Harris *et al*., 2020), Matplotlib (Hunter, 2007), Scikit-learn (Pedregosa *et al*., 2011) and Seaborn (Waskom, 2021). After the LDA, a one-way ANOVA with post-hoc Tukey HSD (Honestly Significant Difference) (Tukey, 1949) test was performed using only characters of ornamentation to verify the discriminant power of the radial ribs in species identification.

Results

From the 29 examined variables, only a subset of five are necessary for species discrimination. Following the minimum BIC searching analysis, are they: the dorsal inflection of the rostrum (7), distance from the posteriormost rib end to the umbonal posterior margin (11), distance from the central point of the valve to the anterior margin in a 45° angle (24), in a 15° angle (22) and in a −30° angle (19).

The analyses using only left valves, only right valves and both valves showed a good separation between the species, as summarized in Table 1. Figure 2 shows the DF classification relative to left valves, with 91% accuracy. Figure 3 shows the DF classification to right valves, with 94% accuracy. Figure 4 is the combined result relative to both valves, with 92.6% accuracy.

The shell ornamentation characters are genus diagnostic and were historically used for species classification. As they were not among the most informative ones, we performed a one-way ANOVA with post-hoc Tukey HSD test specifically for the number of radial ribs. Figure 5 shows the boxplot relative to left valves, and Table 2 summarizes the significance of the difference between species in the observed mean number of radial ribs. These results

Table 1. Summary of the Wilks-Lambda test for the linear discriminant analysis

Analysis	Wilks-Lambda value	df 1	df 2	F value	p-value
Left valves	0.7119	3.0000	66.0000	8.9044	0.00005
Right valves	0.7373	3.0000	64.0000	7.6000	0.0002
Both valves	0.7829	3.0000	199.0000	18.3906	0.000014

The clustering and classification were statistically significant. To perform the statistical test one needs the Wilks-Lambda value, the degrees of freedom of the grouping variable (df 1), the degrees of freedom of the dependent variables (df 2) and the value for test statistic F. The comparison is done using the p-value.

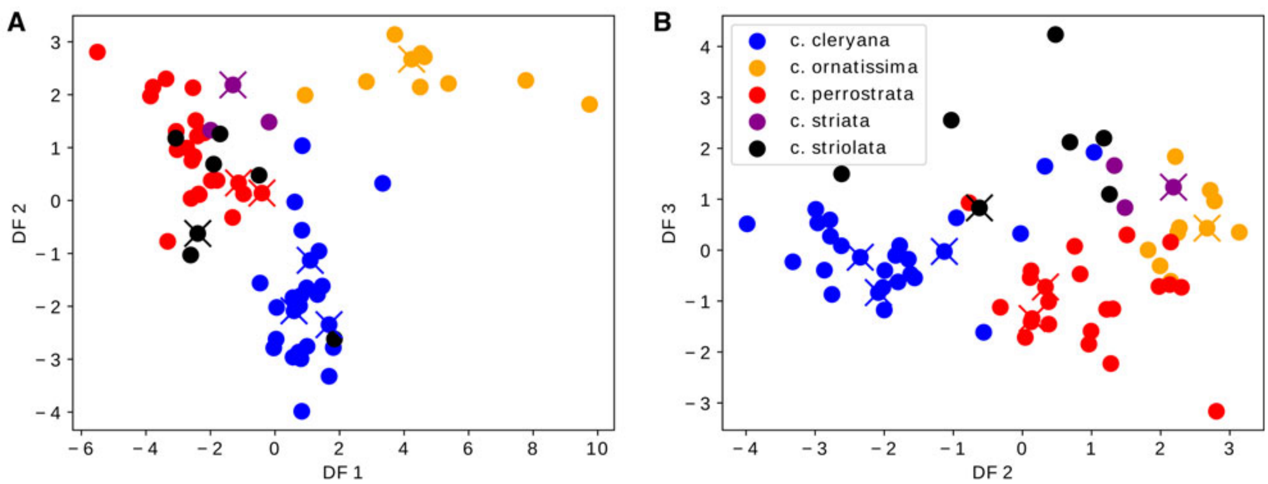

Figure 2. Species separation using the discriminant function obtained following the minimum BIC analysis. This result is based on a dataset composed only by left valves not used in the original training phase and reaches a 91% score. The data points marked with the 'x' are from the types of each species. For better visualization, the three discriminant functions are depicted using two bidimensional scatterplots. (A) The relation between the discriminant functions DF1 (*x*-axis) and DF2 (*y*-axis). (B) The relation between the discriminant functions DF2 (*x*-axis) and DF3 (*y*-axis).

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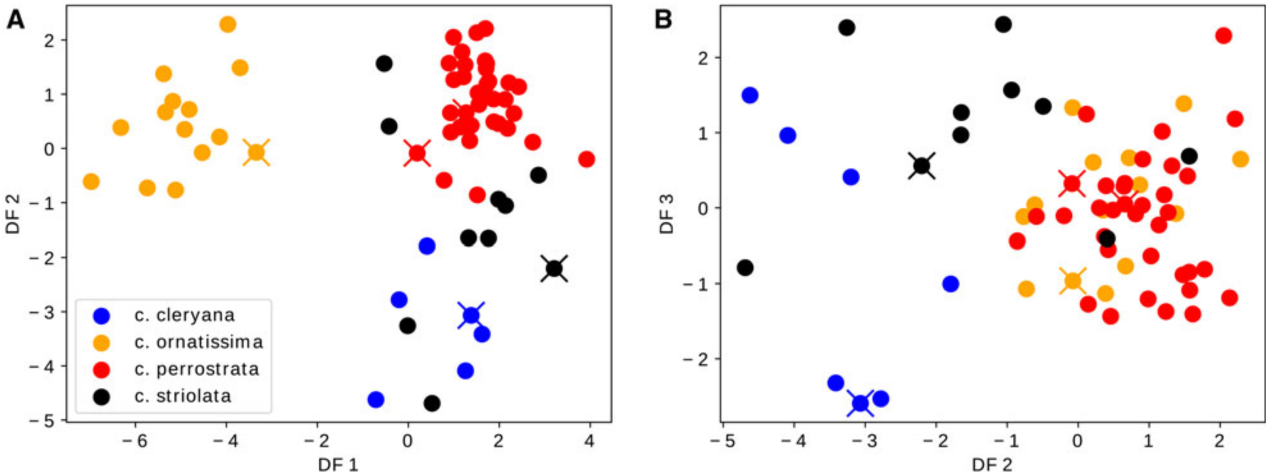

Figure 3. Species separation using the discriminant function obtained following the minimum BIC analysis performed for the left valve. This result uses all right valves and reaches a 94% score. The data points marked with the 'x' are from the types of each species. For better visualization, the three discriminant functions are depicted using two bidimensional scatterplots. (A) The relation between the discriminant functions DF1 (*x*-axis) and DF2 (*y*-axis). (B) The relation between the discriminant functions DF2 (*x*-axis) and DF3 (*y*-axis).

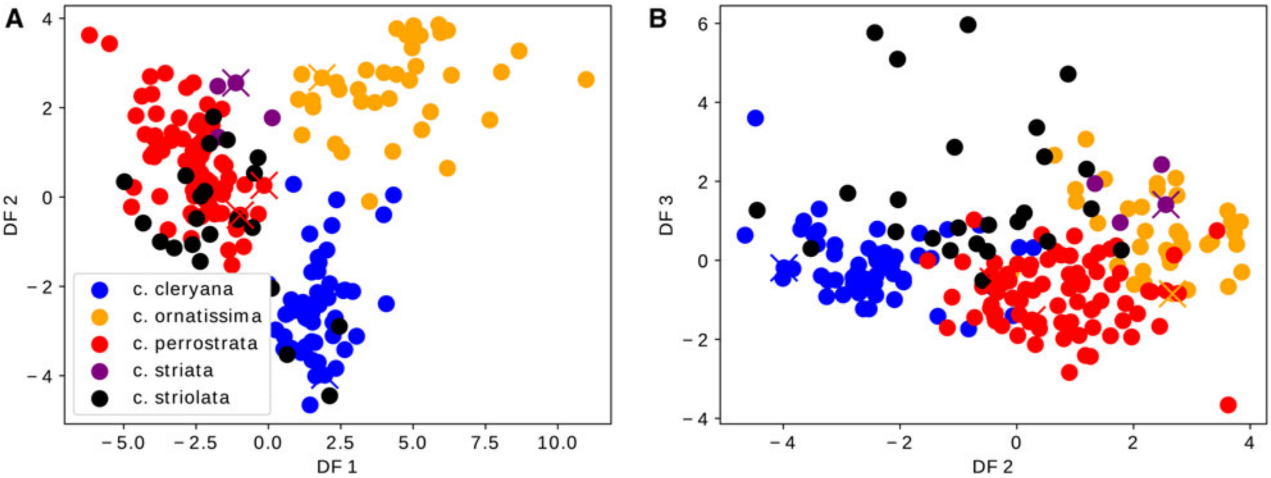

Figure 4. Species separation using the discriminant function obtained following the minimum BIC analysis using both valves jointly, showing a performance of 92.6% score. For better visualization, the three discriminant functions are depicted using two bidimensional scatterplots. (A) The relation between the discriminant functions DF1 (*x*-axis) and DF2 (*y*-axis). (B) The relation between the discriminant functions DF2 (*x*-axis) and DF3 (*y*-axis). The data points marked with the 'x' are from the types of each species.

are replicated for the right valve in Figure 6 and Table 3 and combining both valves in Figure 7 and Table 4.

The weights obtained to calculate the DF are provided in Table 5.

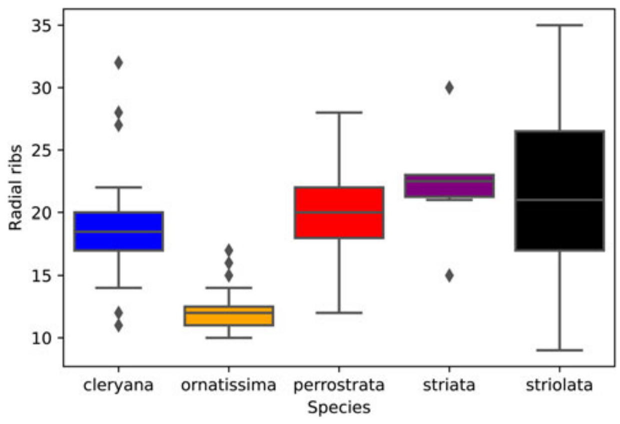

Figure 5. Boxplot of the meristic variable historically used for species classification, the number of radial ribs, considering only left valves. One-way ANOVA with Tukey post-hoc test was applied to verify its discriminant power in species identification.

Discussion

In general, Molluscs have rigid structures that are easy to measure, which facilitates the use of morphometric tools in solving taxonomic problems. Several studies have been using morphometric techniques in the resolution of taxonomic issues (Absalão and de Paula, 2004; Benaim and Absalão, 2011; Souza and Caetano, 2020). The present study uses morphometry not only to discriminate species, but also to understand which variables must be used for this.

Our results determine the smallest set of morphological variables necessary to efficiently discriminate the Brazilian *Cardiomya* at species level. Within these variables, the characters related to the outline of the shell, not to the ornamentation, are the most informative. Previous studies with Cuspidariidae had already demonstrated the importance of contour in the taxonomy of species (Allen and Morgan, 1981; Pacheco, Teso and Pastorino *et al.*, 2022). From the 29 examined variables, only a subset of five is necessary for species discrimination. Are they: (7) the dorsal inflection of the rostrum that reflects the degree to which the rostrum is inclined upwards or downwards (i.e. the angulation of the face). This measure directly influences the individual's shape in the posterodorsal region; (11) distance from the posteriormost

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Table 2. Summary of the one-way ANOVA with Tukey post-hoc test performed using the radial ribs information from the left valves only

A	B	Mean (A)	Mean (B)	Difference	SE	t	P-Tukey
C. cleryana	*C. ornatissima*	18.758065	12.304348	6.453717	0.943038	6.843537	0.001000
C. cleryana	*C. perrostrata*	18.758065	20.130435	−1.372370	0.751652	−1.825806	0.363432
C. cleryana	*C. striata*	18.758065	22.333333	−3.575269	1.651439	−2.164941	0.198915
C. cleryana	*C. striolata*	18.758065	21.800000	−3.041935	1.111433	−2.736948	0.053419
C. ornatissima	*C. perrostrata*	12.304348	20.130435	−7.826087	0.986419	−7.933839	0.001000
C. ornatissima	*C. striata*	12.304348	22.333333	−10.028986	1.770676	−5.663931	0.001000
C. ornatissima	*C. striolata*	12.304348	21.800000	−9.495652	1.281923	−7.407352	0.001000
C. perrostrata	*C. striata*	20.130435	22.333333	−2.202899	1.676589	−1.313917	0.660559
C. perrostrata	*C. striolata*	20.130435	21.800000	−1.669565	1.148471	−1.453729	0.581786
C. striata	*C. striolata*	22.333333	21.800000	0.533333	1.865812	0.285845	0.900000

A and B are the pairs of groups being compared by the statistical test, t is the value of the test statistic and P-Tukey the p-value used for comparison.

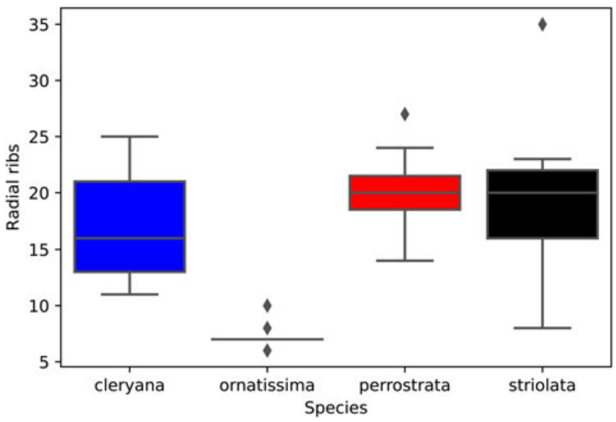

Figure 6. Boxplot of the meristic variable historically used for species classification, the number of radial ribs, considering only right valves. One-way ANOVA with Tukey post-hoc test was applied to verify its discriminant power in species identification.

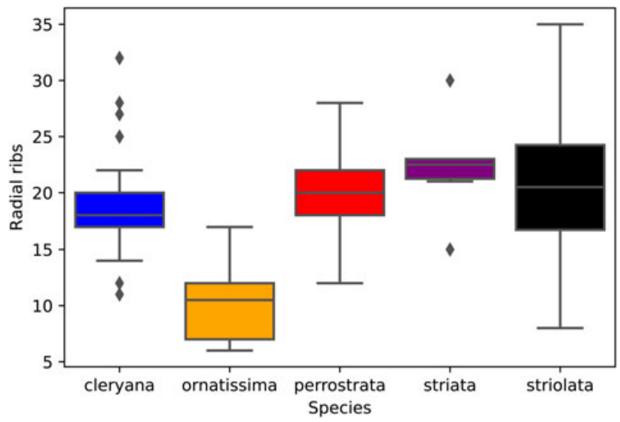

Figure 7. Boxplot of the meristic variable historically used for species classification, the number of radial ribs, considering both valves. One-way ANOVA with Tukey post-hoc test was applied to verify its discriminant power in species identification.

rib end to the umbonal posterior margin, this measurement translates the thickness from the base of the rostrum to the end of the shell flank; and (24, 22, 19) distance from the central point of the valve to the anterior margin in a 45° angle, in a 15° angle and in a −30° angle. These three measurements collectively assess the shape of the anterior part of the shell, more specifically, the degree of anterodorsal descent, the rounding or truncation/straightness of medial part, and the degree of anteroventral extension or rounding.

From a quantitative perspective, one can measure the morphological variables suggested by this work as the most informative ones and directly use the DF provided in Table 5 to identify one of the five described *Cardiomya* species used in the analysis. More than that, and perhaps more powerful taxonomically, one can get hints of new species by observing new groupings formed in the scatterplot that are not explained by the five base species used.

Cardiomya exhibits morphological differences between valves. Left valves tend to have a more extended ventral margin, while right valves tend to have a more elongated posterodorsal region. Our results demonstrated that despite the inequivalve shell, the informative characters remain constant independently of the shell side (i.e. left or right valve). This is a useful result considering that a substantial part of the material deposited in the collections is composed of single valves.

Curiously, although the radial ribs are the most remarkable feature of the genus, they are not informative at species level. As the most informative set of morphological variables for species discrimination surveyed by the LDA included only contour

Table 3. Summary of the one-way ANOVA with Tukey post-hoc test performed using the radial ribs information from the right valves only

A	B	Mean (A)	Mean (B)	Difference	SE	t	P-Tukey
C. cleryana	*C. ornatissima*	17.142857	7.200000	9.942857	1.678861	5.922384	0.001000
C. cleryana	*C. perrostrata*	17.142857	19.857143	−2.714286	1.518587	−1.787376	0.288715
C. cleryana	*C. striolata*	17.142857	19.769231	−2.626374	1.719461	−1.527440	0.428626
C. ornatissima	*C. perrostrata*	7.200000	19.857143	−12.657143	1.131888	−11.182332	0.001000
C. ornatissima	*C. striolata*	7.200000	19.769231	−12.569231	1.389824	−9.043760	0.001000
C. perrostrata	*C. striolata*	19.857143	19.769231	0.087912	1.191277	0.073796	0.900000

A and B are the pairs of groups being compared by the statistical test, t is the value of the test statistic and P-Tukey the p-value used for comparison.

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Table 4. Summary of the one-way ANOVA with Tukey post-hoc test performed using the radial ribs information from both left and right valves

A	B	Mean (A)	Mean (B)	Difference	SE	t	P-Tukey
C. cleryana	*C. ornatissima*	18.594203	10.289474	8.304729	0.795402	10.440918	0.001000
C. cleryana	*C. perrostrata*	18.594203	20.012346	−1.418143	0.645045	−2.198519	0.184057
C. cleryana	*C. striata*	18.594203	22.333333	−3.739130	1.675875	−2.231151	0.172369
C. cleryana	*C. striolata*	18.594203	20.857143	−2.262940	0.882254	−2.564953	0.080803
C. ornatissima	*C. perrostrata*	10.289474	20.012346	−9.722872	0.774195	−12.558685	0.001000
C. ornatissima	*C. striata*	10.289474	22.333333	−12.043860	1.729697	−6.962986	0.001000
C. ornatissima	*C. striolata*	10.289474	20.857143	−10.567669	0.980646	−10.776229	0.001000
C. perrostrata	*C. striata*	20.012346	22.333333	−2.320988	1.665915	−1.393221	0.615473
C. perrostrata	*C. striolata*	20.012346	20.857143	−0.844797	0.863183	−0.978700	0.849570
C. striata	*C. striolata*	22.333333	20.857143	1.476190	1.771316	0.833386	0.900000

A and B are the pairs of groups being compared by the statistical test, t is the value of the test statistic and P-Tukey the p-value used for comparison.

Table 5. Weights for each of the most informative variables obtained by the discriminant analysis

	Measurement				
Species	(7)	(11)	(19)	(22)	(24)
C. cleryana	−4.16	3.06	10.06	−23.83	14.76
C. ornatíssima	20.94	7.46	−8.01	−13.43	2.98
C. perrostrata	−4.96	−4.78	−11.21	28.39	−11.07
C. striata	2.92	−6.38	−5.57	29.38	−21.73
C. striolata	−3.09	−5.32	12.84	7.80	−15.40

These values are used to construct the discriminant function given the values of the morphological characters. By using these values, one can either identify one of the five species used in this work and also provide hints for new species in future analysis by observing groupings formed in the scatterplot that are not explained by the five base species used.

characters, an approach was then carried out including only ornamentation characters. The relevance of ornamentation variability in species discrimination was tested using a one-way ANOVA with post-hoc Tukey HSD hypothesis test specifically including the number of ribs. Except for cases of extreme variation in *Cardiomya ornatissima*, the total number of ribs does not show significant difference between the analysed species.

The fact that most informative characters are associated with the outline, specifically the anterodorsal margin and the rostral curvature, may have a biological explanation underneath. Considering the anterior part of the shell, the specimens can be divided mainly into two groups: (1) those that have a shoulder (*C. striolata*, *C. perrostrata*, *C. striata*) and (2) those that do not have a shoulder (*C. cleryana*, *C. ornatissima*), a shoulder can be defined as an expansion of the dorsal anterior margin (for more details see de Lima *et al.*, 2020). These differences may indicate an eventual occupation of different substrates, where the shoulder provides greater stability while digging and burying in substrates with different granulometries. Likewise, the size and angle of the rostrum determine how far this animal can bury itself without losing contact with the surface. Harper *et al.* (2006) mentioned that the Anomalodesmata inhabit the bottom of unconsolidated substrate, and dig at different levels. Our results reinforce the evidence already pointed out in previous studies (e.g. Harper *et al.*, 2006; Machado *et al.*, 2017) that the depth at which the animal burrows is determined not only by environmental factors, but also by conchological and, consequently, taxonomic factors.

Conclusion

Despite the historically confused taxonomy of *Cardiomya*, a small set of characters related to the shell outline is able to efficiently discriminate Brazilian species. Future studies may extend the use of morphometric tools, a very efficient approach in solving taxonomic problems, to other *Cardiomya* species.

Supplementary material. The supplementary material for this article can be found at https://doi.org/10.1017/S0025315424000031.

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Data availability. The data that support the findings of this study are available from the corresponding author, T. C. de Lima, upon reasonable request.

Author contributions. Tarcilla C. de Lima: project design, material analysis, material photography, data analysis, writing and review. Victor B. B. Mello: statistical data analysis, writing and review. Cléo D.C. Oliveira: project design, writing and review.

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