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Qualitative and Quantitative Characterization of Some Common Bivalves: *Polymesoda bengalensis, Codakia tigerina* and *Anodontia edentula*

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ABSTRACT

For more than a hundred years the morphology of bivalves was an object of research. The best way to explore bivalve morphology is on the shell. The shell provides a wide array of variability and is important for the effective culture of these organisms. In this study, the right and left valve interiors of the three species belonging to the family Cyrenidae (Polymesoda bengalensis) and Lucinidae (Codakia tigerina and Anodontia edentula) were explored for phenotypic variations using Geometric Morphometrics (GM) tools coupled with Canonical Variance Analysis (CVA), Multivariate Analysis of Variance (MANOVA), Relative Warp Analysis (RWA), and Kruskal-Wallis test. Ten (10) anatomical landmark tests were performed – covering the visible morphological characteristics of the internal shell. The analyses showed that the formation of the hinge plate, distance of the pallial line, and the orientation of the muscle scar are significantly different. These features are usually affected by habits and habitats of the particular species. Hence, these characters are better suited for functional morphological analysis and should be incorporated when studying intrapopulation and interpopulation variation.

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INTRODUCTION

In the study of the biological form of bivalves, shells are traditionally used in classifications and taxonomic descriptions. The external form of the shell was the principal character used in molluscan species-level taxonomy including diverse groups. Since shell morphometry and sculpture are regarded as essential for species discrimination [2], a comparative study on three species of bivalves inhabiting different ecological environments was done. These species are Bengali geloina (*Polymesoda bengalensis*) that live in mud flats and estuaries of mangrove areas, and occurring in the Indo-West Pacific from India to Thailand and Celebes, and from the Philippines to northern Australia [3], the pacific tiger lucine (*Codakia tigerina*) commonly known as “bakalan” which are buried in sandy bottoms, often in coral reef areas, from shallow sub littoral waters to a depth of 20 m. and the toothless lucine (*Anodontia edentula*) commonly known as “imbao” which are abundantly distributed in the Indo-West Pacific, from East and South Africa, including Madagascar and the Red Sea, to eastern Polynesia; north to southern Japan and Hawaii, and south to New South Wales [1]. All the three species are locally exploited in the Philippines where the shells are used for decorative crafts or to make lime, and the meat is eaten or chewed with betel nut to make the teeth strong [20]. Since these three species are almost having similar external shell shapes, it is important to have a good qualitative and quantitative measure of the nature of variability in the shell structure. For many years, the study of biological form progressed from qualitative to quantitative. While evaluation of characters is sometimes based on qualitative descriptions of the biological structure [10], a more advanced and recent methodology to effectively quantify shell morphometry is the application of Geometric Morphometric (GM) methods. GM has been successfully applied to distinguish between similar species of bivalves, between wild and aquaculture stocks and between fossil and modern taxa, and also to detect ontogenetic shape changes and to analyze geographic variation in shape [11] thus was applied in the current study.

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This study described and analyzed the internal anatomical patterns of the bivalve shell and to explain morphological differences in relation to its adaptation providing analytical explanations of bivalve shell patterns that could offer additional records in understanding the nature of morphological variability of the bivalve shells.

MATERIALS AND METHODS

Specimen Collection and Preparation of Samples:

The samples were taken from the marshes of Tubod, Lanao del Norte, Philippines. Ninety-one (91) individuals were used for morphometric analyses: 31 specimens of *Polymesoda bengalensis*, 30 specimens of *Codakia tigerina* and 30 specimens of *Anodontia edentula*. Samples were cleaned of their soft tissue before the shells were sun-dried (Figure 1).

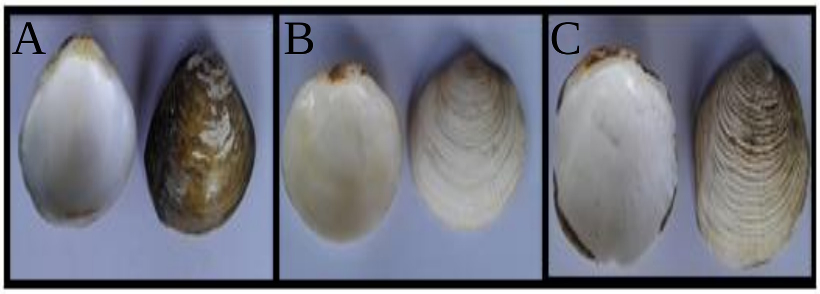

Fig. 1: The internal and external view of (A) *P. bengalensis*, (B) *C. tigerina* and (C) *A. edentula.*

Qualitative and Quantitative Descriptions:

The shells were described based on the following characteristics: shell shape, umbo, ligament position, ligament location, ligament type, hinge line, dentition, musculature, pallial line, and pallial sinus. Qualitative descriptions were then used to correlate the numerical data obtained from GM analysis. To quantify the shell morphometry, a digital image of internal part of the left and right valve of each specimen was taken in a dorso-ventral orientation. On each image, ten landmark points (Figure 2) were marked using tpsDig freeware version 2.2. The number of landmarks was determined by inspection, covering the necessary anatomical points of a typical bivalve shell (Table 1).

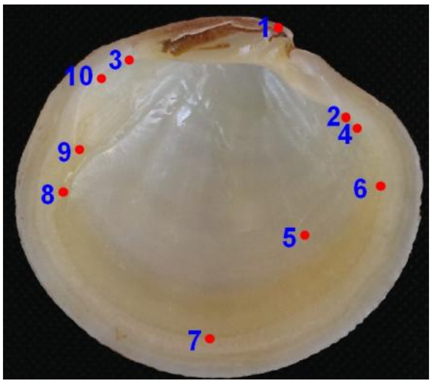

Fig. 2: Assigned landmarks used to describe the internal shell of the three bivalves.

Table 1: Descriptions and types of anatomical landmarks used to describe the three species of bivalve in terms of left valve and right valve internal morphology.

Anatomical Landmarks	Configuration
1	Umbo
2	Ventral anterior end of hinge plate
3	Ventral posterior end of hinge plate
4	Dorsal tip of anterior adductor-retractor muscle scar
5	Ventral tip of anterior adductor-retractor muscle scar
6	Anterior end of the pallial line
7	Deepest point of pallial line
8	Posterior end of the pallial line
9	Ventral tip of posterior adductor-retractor muscle scar
10	Dorsal tip of the posterior adductor-retractor scar

The different coordinates produce by tpsDig v.2.2 were subjected to the program tpsRelw freeware version 1.46 [10, 17] which this program shows the Relative Warps among this three specimens. Relative warp (RW) analysis using all shape variables were used to provide an ordination of all the specimens in a morphological space [11]. All relative warp scores were subjected to Paleontological Statistics (PAST) software version 1.91 [5] for further analysis. Canonical Variance Analysis (CVA) was used for scatter plot elucidation to compare patterns of population variation. Kruskal-Wallis Test was then used to determine if there were significant differences on the anatomical structures/landmarks. Other graphical presentation including box plots and histograms were also incorporated to provide a compact view of where the different populations are centered and how they are distributed over the range of the variable. Lastly, correlation analysis was employed to determine whether morphological descriptions and the shapes of the shell are significantly correlated or not.

RESULTS AND DISCUSSIONS

Qualitative descriptions:

The general phenotypic features of the shell of the three species of bivalves are shown in Table 2. These characters were used to identify the species [7] as employed in taxonomic keys [14].

Table 2: Characters described of the shells of three bivalve species.

Characteristics	*Polymesoda bengalensis*	*Codakia tigerina*	*Anodontia edentula*
Shell Shape	Subtrigonal to rounded	Subcircular	Rounded
Umbo	Orthogyrous	Prosogyrous	Prosogyrous
Lunule	Small, depressed	Small, depressed	Moderately large, slightly depressed
Ligament Position	External	External	External
Ligament location	Opisthodetic	Opisthodetic	Opisthodetic
Ligament Type	Parivincular	Parivincular	Parivincular
Hinge line	Arched	Arched	Arched
Dentition	Heterodont, with cardinal and lateral teeth	Heterodont, with cardinal and lateral teeth	Desmodont, without teeth
Musculature	Anisomyarian	Anisomyarian	Anisomyarian
Pallial line	Present	Present	Present
Pallila sinus	Absent	Absent	Absent

The shell shape of the three species was observed to be different from each other suggesting distinct morphological adaptations. Since most species of bivalves inhabit the intertidal zone that require high mechanical stability [9, 13], the differences in the shell outline could be an effective adaptation for such type of habitat. Aside from being adapted to intertidal zones, most bivalves are also burrowers [21], those with more streamlined shapes dig deeper. However, the umbo in *P. bengalensis* is orthogyrous, an uncommon feature among other burrowing bivalves where typically the beaks are pointed towards the anterior of the shell [12] as evident in *C. tigerina* and *A. edentula* suggesting that the differences can be genetic in nature. Examination of the lunule, a heart shaped impression on the external side of the hinge that is anterior to the umbo, was found to be depressed in the three species. The depressed lunule is not involved in the burrowing but it is important in taking the weight away from the front and shifting the center of the gravity backward and making assymetric rocking motion of bivalves more effective [15]. Its presence in the three species may suggest shaking of their shells to loosen the sand and to ease their movement through the sediment while burrowing. The valves of the three species were similar being an equivalve held together by an elastic ligament leaving a scar on the hinge. The ligaments were also similar for the three species being opisthodethic and parivincular indicating external development [13]. The same observation was also true to the hinge line of the three species which is arched. The hinge was found to have interlocking ridges called the dentition and was found to differ in the three species. The individual ridges or teeth of *P. bengalensis* and *C. tigerina* are heterodont having cardinal teeth and lateral teeth either in front and/or behind beak, while *A. edentula* is desmodont usually lacking well defined teeth [8]. The two valves were observed to be articulated to the soft body by adductor muscles that produce a scar on the interior surface. The three species are dimyarian having two scars on each valve [19]. The three species are integripalliate since they don’t have a pallial sinus [4].

Quantitative Descriptions:

CVA scatter plots of the three bivalve species were clustered from different quadrants (Figure 3) indicating the shapes of the shells were significantly different. The clustering of the individual samples is evidently consistent in both the left and right internal valves. Pairwise comparisons between species are shown in Table 3 indicating the differences observed among the three species were significant.

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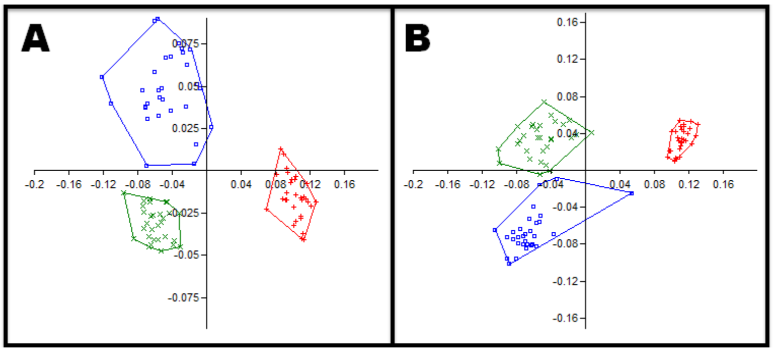

Fig. 3: CVA scatter plot of the (A) left and (B) right interior valves of *Polymesoda bengalensis* (red), *Codakia tigerina* (blue), and *Anodontia edentula* (green).

Table 3: Pairwise comparison of the three species multivariate analysis of variance (MANOVA) for the three bivalve species.

Left interior valve	*P. bengalensis*	*C. tigerina*	*A. edentula*
P. bengalensis	-	1.08287E-23*	4.48528E-40*
C. tigerina	3.24861E-23*	-	2.85416E-18*
A. edentula	1.34559E-39*	8.56249E-18*	-
Right interior valve	*P. bengalensis*	*C. tigerina*	*A. edentula*
P. bengalensis	-	1.8447E-26*	5.08511E-30*
C. tigerina	5.5341E-26*	-	1.27838E-16*
A. edentula	1.52553E-29*	3.83514E-16*	-

Legend: *significant value(s), Bonferroni corrected (lower values)\uncorrected (upper values)

The variations observed within and between species using the method of relative warps [14] demonstrate five and four significant relative warp scores for the left and right internal shells respectively. The variations are shown in the form of plots and histograms for the left (Figure 4A) and right (Figure 4B) valves. Variation percentage and detailed differences in morphological variations on different axes of the significant warps are discussed in Table 4 and Table 5.

Table 4: Left internal valve percentage variance and over all morphological variation of the three species as explained by significant relative warps.

Relative warps	Negative axis	Positive axis
RW 1 (51.36%)	• The distance between the dorso-anterior adductor-retractor muscle scar away from the anterior end of the pallial line. • The ventral tip of the anterior adductor-retractor muscle scar closer to the deepest point of the pallial line. • Longer distance between the posterior end of the pallial line and deepest point of the pallial line. • The distance between the ventral-posterior adductor-retractor muscle scar away from the posterior end of the pallial line. • The over all hinge plate is slightly curved. • The umbo is depressed. • The distance between dorsal tip of anterior adductor-retractor muscle scar and ventral tip of anterior adductor-retractor muscle scar is longer.	• The ventral-anterior tip of the adductor-retractor muscle scar joins together with the anterior end of the pallial line. • Deepest point of the pallial line has shorter distance with the posterior end of the pallial line. • The ventral-anterior adductor-retractor muscle scar has longer distance to the deepest point of the pallial line. • Posterior end of the pallial line is compressed with the ventral-posterior adductor-retractor muscle scar. • The over all hinge plate pronouncely curved. • The distance between dorsal tip of anterior adductor-retractor muscle scar and ventral tip of anterior adductor-retractor muscle scar is shorter.
RW 2 (16.82%)	• Closer distance between posterior end of the pallial line and ventral tip of posterior adductor-retractor muscle scar. • The ventral tip of anterior adductor-retractor muscle scar moves away from the anterior end of the pallial line. • The ventral posterior end of the hinge plate and ventral tip of the posterior adductor-retractor scar moves apart from each other.	• Ventral posterior end of the hinge plate joins together with the dorsal tip of the posterior adductor-retractor muscle scar. • The ventral anterior end of the hinge plate is compressed with the dorsal tip of anterior adductor-retractor muscle scar. • Ventral tip of anterior adductor-retractor muscle scar is compressed with the anterior end of the pallial line.
RW3 (7.57%)	• Ventral and posterior hinge plate are closer together. • Umbo is depressed.	• The distance between the ventral posterior end of the hinge plate is closer to the tip of the posterior adductor-retractor muscle scar. • Ventral tip of posterior adductor-retractor muscle scar closer to both posterior end of the pallial line and tip of the posterior adductor-retractor muscle scar.
	• The distance between the dorsal and ventral tip of	• Distance of the ventral posterior end of

RW4 (5.17%)	anterior adductor-retractor muscle scar is closer. • Ventral posterior end of the hinge plate away from the tip of the posterior adductor-retractor scar.	hinge plate is closer to the tip of the posterior adductor-retractor muscle scar. • Ventral tip of anterior adductor-retractor muscle scar has closer distance with anterior end of the pallial line.
RW5 (5.09%)	• Closer distance between posterior end of the pallial line and ventral tip of posterior adductor-retractor muscle scar. • The ventral posterior end of hinge plate and the tip of the posterior adductor-retractor muscle scar away from each other. • The umbo is slightly depressed.	• The anteriro end of the pallial line moves closer to both dorsal and ventral anterior adductor-retractor muscle scar. • The distance between posterior end of the pallial line apart from that of the ventral tip of posterior adductor-retractor muscle scar. • The anterior margin is compressed.

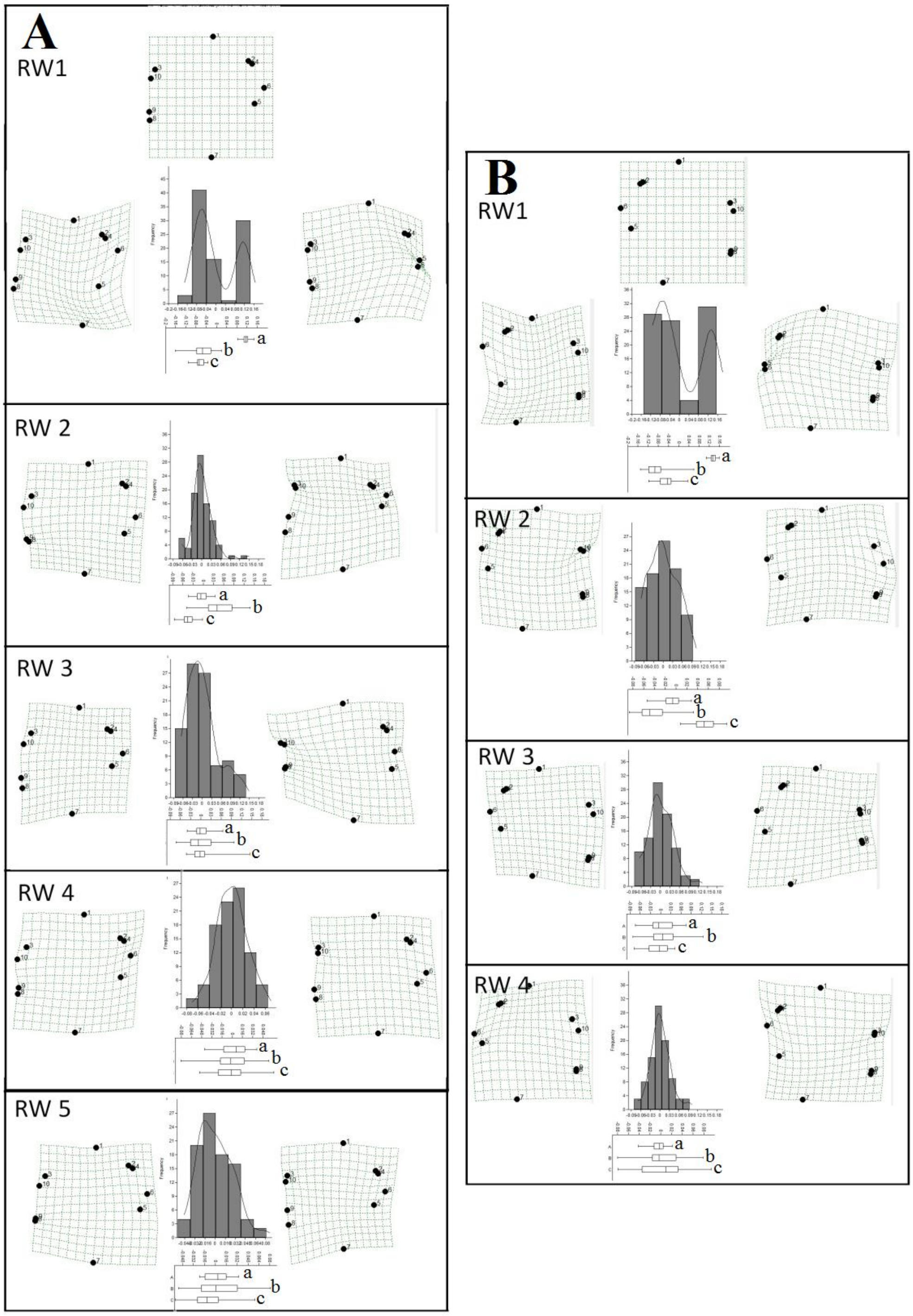

Fig. 4: Relative warp box plots and histogram showing variations in the (A) left valve (B) right valve of the three species of bivalves: *Polymesoda bengalensis* (a), *Codakia tigerina* (b), *Anodontia edentula* (c).

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Table 5: Right internal valve percentage variance and over all morphological variation of the three species as explained by significant relative warps.

Relative warps	Negative axis	Positive axis
RW 1 (59.08%)	• The umbo is depressed • Distance between the ventral tip of the anterior adductor-retractor muscle scar and anterior end of the pallial line away from each other. • Shorter distance between the ventral tip of anterior adductor-retractor muscle scar and deepest point of pallial line. • The distance between the ventral tip of posterior adductor-retractor muscle scar and dorsal tip of the posterior adductor-retarctor muscle scar is longer.	• Ventral tip of anterior adductor-retractor muscle scar joins with the anterior end of the pallial line. • The distance between the ventral posterior end of hinge plate and tip of the posterior adductor-retractor muscle scar is closer. • The hinge plate is pronouncedly curved. • The distance between the ventral tip of posterior adductor-retractor muscle scar and dorsal tip of the posterior adductor-retarctor muscle scar is shorter.
RW 2 (11.38%)	• Ventral posterior end of the hinge plate joins together with the tip of the posterior adductor-retractor muscle scar. • The distance between the dorsal tip of anterior adductor-retractor muscle scar is closer to the anterior end of the pallial line.	• Ventral posterior end of hinge plate and tip of the posterior adductor-retractor muscle scar away from each other. • Distance of the ventral tip of anterior adductor-retractor muscle scar is slightly closer with the deepest point of pallial line.
RW3 (9.25%)	• The distance between the dorsal tip of anterior adductor-retractor muscle scar is closer to the anterior end of the pallial line. • Closer distance between deepest point of pallial line and anterior end of pallial line.	• Tip of the posterior adductor-retractor muscle scar moves closer to the ventral posterior end of hinge plate and ventral tip of posterior adductor-retractor muscle scar.
RW4 (5.96%)	• Distance of the ventral posterior end of hinge plate moves closer to the dorsal tip of anterior adductor-retractor muscle scar. • Ventral tip of anterior adductor-retractor muscle scar and anterior end of the pallial line closer to each other. • Distance between ventral anterior end of hinge plate and dorsal tip of anterior adductor-retractor muscle scar are compressed with each other.	• Ventral posterior end of the hinge plate is closer to the tip of the posterior adductor-retractor muscle scar. • The distance of the ventral tip of anterior adductor-retractor muscle scar away from the anterior end of the pallial line. • Dorsal tip of anterior adductor-retractor muscle scar has closer distance with the anterior end of the pallial line.

Relative Warp (RW) 1 of the left interior valve is bimodal, this means having two peaks at the positive and negative values. The range of *P. bengalensis* spreads along the positive values of the axis, suggesting that the sample reflects the morphologies explained in the positive plane of the RW. While the ranges of *C. tigerina* and *A. edentula* are on the negative values of the axis, implying that these species resemble the morphologies of the negative axis of RW1. Box plot of RW2 shows that the range of *C. tigerina* is situated in the positive axis but also extends slightly to the negative axis while the other two is almost uniformly distributed towards zero suggesting a much closer resemblance to the mean shape. The RW3 to RW5 box plot graphs for the three species are relatively similar in distribution that the three population fall in the consensus morphology, which further indicates that most individuals have morphologies identical or similar to the consensus.

For the right valve, a bimodal RW1 distribution of the population in the first relative warp strongly suggests two separate normally distributed populations. *P. bengalensis* draw towards the positive axis, while *C. tigerina* on the negative but slightly deviates to the positive axis, and *A. edentula* lies along point zero. Histogram for RW2 is unimodal which shows that the range of *P. bengalensis* is almost uniformly distributed in the mean or zero value of the horizontal plane. Furthermore, the range of *C. tigerina*, as shown in the boxplot, is found lying on the negative axis but slightly deviates to the the positive values of the axis. While, the range of *A. edentula* is located in the positive values. Like RW2, histograms of RW3 and RW4 are both unimodal which shows that both are uniformly distributed in the negative and positive values, with most individuals positioned at zero value. Pairwise comparison of the morphological differences in shell shapes between the three species as shown by the significant relative warps were tested using Kruskal-Wallis test (Table 6). For the left shell, all the variations observed between *P. bengalensis* and *C. tigerina*, and *P. bengalensis* and *A. edentula* in RW1 are highly significant but not between *C. tigerina* and *A. edentula*. For RW2, all the variations observed in the three species are significant. For the right valve, variations in shell shapes between species described in RWs 1 and 2 are significantly different.

Table 6: Results of the Kruskal-Wallis Test for significant differences in the mean morphologies of the three species.

Left interior valve				Right interior valve			
RW1	A	B	C	RW1	A	B	C
A	-	2.07E-11*	2.07E-11*	A	-	2.07E-11*	2.0E-11*
B	6.2E-11*	-	0.1393	B	6.2E-11*	-	9.8E-06*
C	6.2E-11*	0.4179	-	C	6.2E-11*	2.95E-05*	-
RW2	A	B	C	RW2	A	B	C
A	-	3.961E-07*	1.5E-08*	A	-	2.85E-06*	4.9E-11*
B	1.2E-06*	-	3.2E-10*	B	8.5E-06*	-	8.2E-11*

C	4.481E*	9.477E-10*	-	C	1.5E-10*	2.44E-10*	-
RW3	A	B	C	RW3	A	B	C
A	-	0.5398	0.5303	A	-	0.7076	0.4841
B	1	-	0.7283	B	1	-	0.3403
C	1	1	-	C	1	1	-
RW4	A	B	C	RW4	A	B	C
A	-	0.6086	0.3987	A	-	0.6443	0.3338
B	1	-	0.9293	B	1	-	0.9941
C	1	1	-	C	1	1	-
RW5	A	B	C				
A	-	0.5935	0.3275				
B	1	-	0.05188				
C	0.09826	0.1556	-				

Legend: *significant value, A – *Polymesoda bengalensis*, B – *Codakia tigerina*, C – *Anodontia edentula* Bonferroni corrected (lower values)\uncorrected (upper values)

Correlation analysis of the morphological characters and shapes of the bivalve shells are negatively correlated (Table 7). It has been accounted that characterization of the internal shells can be strengthened using geometric morphometric analysis. Results of the descriptions of the morphology of the shells of the three species obtained from the significant RWs are summarized in Table 8.

Table 7: Correlation analysis of the morphological patterns and quantitative descriptions of the three species of bivalves.

Variables	Left valve		Right valve	
	r value	p value	r value	p value
shell shape	-0.85161	1.0663E-26	-0.73073	2.0074E-16
Umbo	-0.94995	9.5159E-47	-0.93855	6.819E-43
Lunule	-0.52536	8.9548E-08	-0.32635	0.0015939
Dentition	-0.523536	8.9548E-08	-0.32635	0.0015939

Table 8: Over-all morphological descriptions of the interior shell of the three bivalves.

Polymesoda bengalensis

- The over all hinge plate is prouncedly curved.
- The ventral-anterior tip of the adductor-retractor muscle scar joins together with the anterior end of the pallial line.
- The ventral-anterior adductor-retractor muscle scar has longer distance to the deepest point of the pallial line.
- Posterior end of the pallial line is compressed with the ventral-posterior adductor-retractor muscle scar.
- The distance between the ventral posterior end of hinge plate and dorsal tip of the posterior adductor-retractor muscle scar is closer.
- The distance between dorsal tip of anterior adductor-retractor muscle scar and ventral tip of anterior adductor-retractor muscle scar is shorter.
- The distance between the dorso-anterior adductor-retractor muscle scar apart from the anterior end of the pallial line.
- Closer distance between posterior end of the pallial line and ventral tip of posterior adductor-retractor muscle scar.
- The distance between the ventral tip of posterior adductor-retractor muscle scar and dorsal tip of the posterior adductor-retarctor muscle scar is longer.

Table 8: Continuation…

Codakia tigerina

- The over all hinge plate is slightly curved.
- The umbo is depressed, anteriorly pointed.
- The distance between the ventral-posterior adductor-retractor muscle scar moves away from the posterior end of the pallial line.
- The ventral tip of the anterior adductor-retractor muscle scar moves closer to the deepest point of the pallial line.
- Longer distance between the posterior end of the pallial line and deepest point of the pallial line.
- The distance between dorsal tip of anterior adductor-retractor muscle scar and ventral tip of anterior adductor-retractor muscle scar is longer.
- Ventral posterior end of the hinge plate joins together with the dorsal tip of the posterior adductor-retractor muscle scar.

Anodontia edentula

- The over all hinge plate is slightly curved.
- The distance between the ventral-posterior adductor-retractor muscle scar apart from the posterior end of the pallial line.
- Ventral posterior end of hinge plate and dorsal tip of the posterior adductor-retractor muscle scar away from each other.
- The distance between the ventral-posterior adductor-retractor muscle scar away from the posterior end of the pallial line.
- The distance between dorsal tip of anterior adductor-retractor muscle scar and ventral tip of anterior adductor-retractor muscle scar is longer and thinner.
- Ventral posterior end of the hinge plate joins together with the dorsal tip of the posterior adductor-retractor muscle scar.
- The distance between the ventral tip of posterior adductor-retractor muscle scar and dorsal tip of the posterior adductor-retarctor muscle scar is shorter.

Results show that the differences are focused on the hinge plate formation, muscle scar position and distance of the pallial line. Differences in the hinge plate are due to dentition. Dentition in *P. bengalensis* and *C. tigerina* is heterodont with two to three wedge-shaped cardinal teeth set in the center near the umbones. While desmodont dentition, very small or completely absent teeth, in *A. edentula*. This could be the possible reason for the existence of pronouncedly curved hinge plate of *P. bengalensis* and slight curved hinged for both *C. tigerina* and *A. edentula*. In connection with dentition, the adductor muscle also help the shell to close more efficiently. A system of paired adductor muscles, one at the anterior end and the other at the posterior, is best suited. Sometimes, this muscle leaves a distinctive scar on the internal surface of the shell [16]. Accordingly, differences in the orientation and position of the muscle scar could be affected by the adductor muscles. The larger the muscle scar the larger the adductor muscle attached to it. In majority of bivalves, the posterior portion of the body shell are bigger than the anterior. As a result, the posterior muscle requires to pull stronger and so must be bigger [16]. The same condition is also observed in *C. tigerina* wherein enlargement of the adductor scar is evident. In addition, the pallial line is a mark on the inner surface of a bivalve shell more or less parallel with the margin caused by the attachment of the mantle [6]. Thus, differences in the pallial line could be attributed to the attachment of the mantle into the bivalve shell. In deep burrowers, the pallial line show a pallial sinus in order to lengthen the muscles of a retractable siphon [18]. Since the three bivalves do not have pallial sinus, this may imply that they live just under the surface of the substrate. This is also supported by the moderately rounded or circular shell outline of the three species.

Conclusions and recommendations:

Based from the results, differences in the hinge plate, pallial line, and muscle scar are found to be significant. It has been found that differences in the hinge plate is affected by dentition, while muscle scar is associated with the adductor muscles attaching to it, and the pallial line is attributed to attachment of the mantle into the bivalve shell. These features are usually affected by habits and habitats of the particular species. Furthermore, to fully understand the mechanism of differences observed in the present study, it is highly recommended to conduct research on functional morphological analysis of bivalves. The ecological parameters and habitat of the bivalves should also be noted to effectively explain the reason behind the variability.

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