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Interior shell patterns among the Spondylid species (Bivalvia: Spondylidae) in Mindanao, Philippines

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Abstract. *Ruaza FJC, Maturan DC, Bustillo E. 2024. Interior shell patterns among the Spondylid species (Bivalvia: Spondylidae) in Mindanao, Philippines. Biodiversitas 25: 2901-2906.* The variations among the species of the *Spondylus* were assessed based on its interior shell pattern using landmark-based geometric morphometry. A total of 200 specimens were subjected to analysis. Samples of the Spondylid species were collected and photographed, and 15 landmarks from internal shell morphology were quantified and analyzed. The landmarks include the umbo, teeth, size of the muscle scar, and the pallial sinus. Multivariate analysis of variance revealed significant differences in internal shell characters among Spondylid species across sampling sites ($p<0.05$). Canonical Variance Analysis (CVA) effectively differentiated the local Spondylid species into distinct clusters. In addition, the relative warps captured the most significant sources of variation in the morphological characters analyzed, leading to effective differentiation between the groups or populations of the species. The most distinguishing characteristics among the species are the distance of the pallial line to the ventral tip of the adductor muscle scar and the size of the cardinal tooth. The internal shell characters among the Spondylid species exhibit notable disparity despite their great morphological similarity. These shell characters can be used in the identification while conservation efforts are still in the initial stage of development. The presence of notable dissimilarities in the internal shell characteristics among the Spondylid species indicates that even slight deviations can result in noticeable morphological distinctions. This discovery enhances the understanding of the species divergence within this group and underscores the significance of incorporating internal shell characteristics into taxonomic and ecological investigations.

Keywords: Landmark-based morphometry, Lianga Bay, multivariate analysis, *Spondylus*

Abbreviations: CVA: Canonical Variance Analysis, LGU: Local Government Unit, RW: Relative Warp

INTRODUCTION

The Lianga Bay Surigao del Sur in the Philippines has abundant spiny oysters (genus *Spondylus*) in the local market, restaurants, and resorts. Economically, it becomes a good source of income for fishers living near the coastal areas of the Bay. Besides its pleasant taste compared to other oyster meat, it attracts more tourists to the province because of its delicious oyster meat. However, anecdotal observation is that the unregulated, uncontrolled, and constant harvest of the spiny oyster is now being threatened. The oyster catch in the province has drastically declined. In 2016- 2019, it was reported (Ruaza and Ilano 2021) that the *Spondylus* fishery in Lianga Bay was already exploited. They recommended immediate action in ecological, economic, and legal aspects in the *Spondylus* fishery in the Bay. The unregulated, uncontrolled, and constant harvest of the young and adult spiny oysters makes the resource exploited. The Local Government Unit (LGU) is in the initial stage of crafting action in ecological, economic, and legal aspects in the fishery of *Spondylus* in Lianga Bay Surigao del Sur. The over-exploitation of this important reef bivalve could lead to an imbalance in the ecosystem where they play a vital role. Being both ecologically and economically important, the threats to this reef bivalve need immediate attention.

However, we cannot conserve what we do not know, considering these important local oysters has still no established taxonomy. The *Spondylus* is the only genus in the family Spondylidae. This species inhabits rocky reef areas from the intertidal area to 5- 25 meters deep. Many taxonomic literatures in the *Spondylus* have been extremely different in their nomenclature. In the Eastern Pacific Ocean, the Spondylid taxonomy has many revisions and updates, reflecting the evolving understanding of these species (Lodeiros et al. 2016). Some of the literature has many revisions of names for a given species (Rocha et al. 2015).

Determining the variability among the local Spondylid species is the paper's primary aim, using inexpensive, reliable, and simple methods using morphometric approaches. Using expensive methods such as molecular techniques and other morphological approaches creates a better conclusion but remains ambiguous for certain taxa. The landmark-based geometric morphometry is a low-cost technique. It was designed to facilitate high-resolution analysis of morphological traits, which can be crucial for understanding evolutionary relationships, ecological interactions, and species identification (Morán et al. 2018; Yang et al. 2022). Also, this versatile tool can significantly contribute to morphological research. Its ability to provide

detailed and quantitative shape analysis makes it an indispensable method for scientists working with diverse biological datasets. It is used to find variations in the shape and size of many biological structures in an extensive range of organisms (Taglioretti et al. 2014; Shu et al. 2022; Liu et al. 2024).

This study is the first to report the morphometry of the *Spondylus* species in this field of science. This study analyzed and determined the variability of the anatomical structure and landmarks of the interior shell patterns (left valve) among the local Spondylid species in Mindanao, Philippines. The interior shell was focused instead of the external shell because it is difficult to find a sufficient number of distinct landmarks in the bivalve species (Lee et al. 2017). The Spondylid species comprises highly dense epibionts attached to the shell's surface because of their generally large intra-specific variability. The taxonomy of *Spondylus* is under permanent revision, and the potential for hybridization is assumed. According to Rocha et al. (2015), the absence of a well-documented taxonomic list for bivalves often causes the most basic problems, like difficulty determining the valid name for a taxon.

This study will bridge the gaps and issues regarding the uncertainty of *Spondylus* taxonomy. Morphometric studies can help provide additional evidence for or against a specific taxonomic group. By analyzing the physical characteristics of organisms, morphometry studies can identify subtle differences in shape and size that may be useful for species. This paper can provide valuable information to fishery scientists and managers, helping them make more informed decisions about managing and conservating *Spondylus* populations.

MATERIALS AND METHODS

Study area

The Lianga Bay, Surigao del Sur, Philippines, is famous for the region's spiny oyster *(Spondylus)* fishery. The expensive and high demand for its meat to the local markets and its beautiful shells were used as crafts and jewelry compared to other shells when properly polished. However, their exploitation has caused a drastic decrease in natural populations, leading the Local Government Unit to act immediately on the restrictions on *Spondylus* fishing. The Bay consists of 60 Barangays with 36 coastal Barangays. The Lianga Bay municipalities occupy a total land area of 1,007.50 km^2. It is located in the central part of the province of Surigao del Sur and lies within a geographical coordinate of 8°34'00" and 8°25'06" latitude and 125°59'00" and 126°22'00" longitude. It is bounded on the north by the Pacific Ocean (Figure 1).

Field method

Sample collection and processing

The *Spondylus* specimens were sourced partly from the gleaners who collect them using basic implements. Additional samples were collected during our field sampling at the coastal Barangays of Marihatag, San Agustin, Lianga, and Barobo. Afterward, the collected specimens were brought to Surigao del Sur State University, the Lianga Campus, at the Biology Laboratory for processing. The live Spondylid was initially narcotized with a magnesium chloride solution of 3.5% in seawater. The samples were cleaned to detach the epibionts on the surface of the shells.

The local Spondylid species subjected to geo morphometry

Four (4) species, including the two morphotypes of *Spondylus*, were qualitatively diagnosed in detail. The spines were characterized as broad, spathate, and fine interstitial spines. The examination of the valves was also established: the left valve has the adductor muscle scar mostly to the left of the midline, and the right valve has a scar mostly to the right of the midline. Also, the hinge teeth size and color in the left valve were examined. Likewise, the color of the marginal band around the circumference of the inner margin of the shell was also noted.

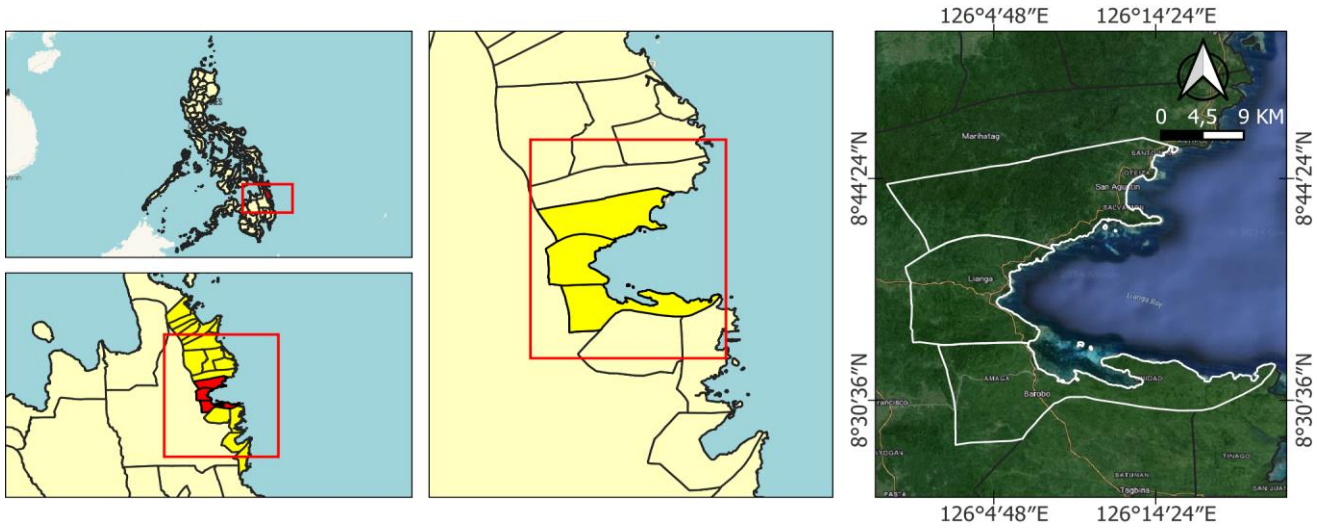

Figure 1. Map of the study area in Lianga Bay: Barobo, Lianga and San Agustin, Surigao del Sur, Philippines

Inner shell diagnosis: Landmark-based geometric morphometry analysis

Shell specimens were mounted on modeling clay to establish standard orientation before photography or measurement. The scale bar (ruler) was attached to the modeling clay since it is essential to compute the meristic presentation of various landmark configurations. The upper valves were photographed (DSLR Canon EOS750D) dorsoventrally in a constant position where all internal shell structures are clear and distinct, with the umbo oriented vertically and upward.

All digitally photographed samples were transferred to a computer for storage and enhancement using photo editing software (Adobe Photoshop). Each shell yielded 15 landmarks (Figure 2) on its interior shell patterns. The establishment of these landmarks was based on the study of Boretto et al. (2014), the shell morphometric variations in Argentina clam (*Ameghinomya antiqua*) from the mid-Pleistocene. The landmarks include the umbo, teeth, size of the muscle scar, and the pallial sinus. The edited images were digitized using the TPS software (TPSDig 2232) to obtain the landmarks data. Afterward, images from TPSDig were uploaded to PaSt v3.01 (Hammer et al. 2001) to produce a variety of coordinates. This software was packaged with geometric and multivariate analyses, including the relative warp, thin plate splines, and warps (2D). The scores were directly analyzed using the MANOVA and Canonical Variates Analysis (CVA).

RESULTS AND DISCUSSION

Landmark-based geometric morphometry

A total of 200 specimens were subjected to landmark-based geometric morphometric analysis. The sample sizes ranged from 50 individuals per species. Distinct clusters among the four (4) Spondylid species of the Bay were noticed when projected onto two- dimensional plane (Figure 3) as defined by their relative warp coordinates. The *S. squamosus* (pink dots) population was mainly clustered at the negative x-axis and slightly overlapped with the *S. limbatus* (blue dots). While the *S. versicolor* (red dots) population was located at the positive y-axis, and almost half of the species overlapped with *S. limbatus* (blue). The *S. varius* (green dots) was mainly clustered in the fourth quadrant.

The CV axis 1 and 2 accounted for 87.4 % of the total variation (Table 1) and the distinct separation of the sample species. This suggests that the first CV accounts for substantial variation in the dataset and represents the most significant axis of differentiation among the Spondylid species. While individual measurements of internal shell characters differed only slightly, the collective difference, when analyzed collectively using CVA, resulted in the clustering of the specimens into species within minimal tools. It was observed that most of the attributes of the *Spondylus* shared the same character within. The slight overlap in the positive y-axis (Figure 3) of S. versicolor, S. limbatus, and *S. squamosos* showed that some shell characters/landmarks have similar morphological attributes. Among the *Spondylus* species, the *S. varius* is the most distinguishable Spondylid species. Aside from its exceptional size, which is relatively large, it has distinct spines, is pure white on the outside and inside, and has color red-orange spots on its umbo and the cardinal area of its hinge.

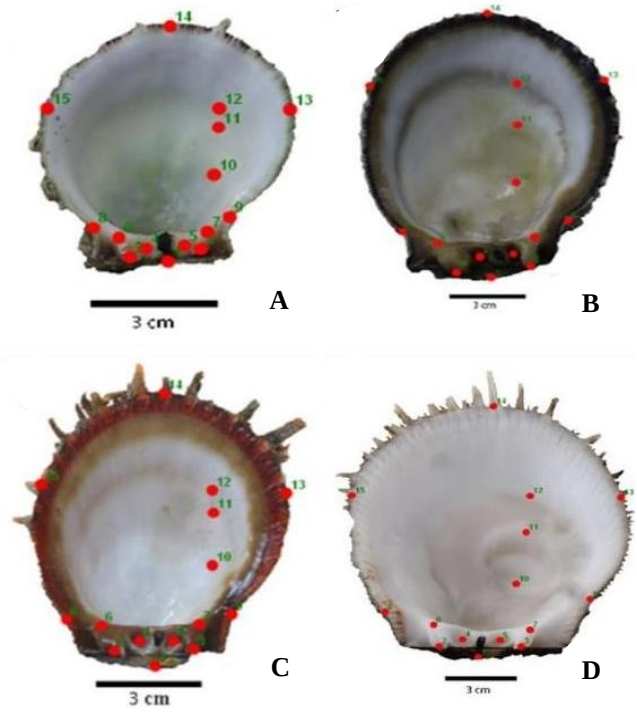

Figure 2. Landmarks used to describe the left valve internal morphology of the Spondylid species: (A) *S. squamosus*; (B) *S. limbatus*; (C) *S. versicolor*; (D) *S. varius*: *Landmark configuration*: 1. umbo; 2. dorsal tip of anterior cardinal tooth; 3. dorsal tip of anterior cardinal tooth; 4. Posterior socket; 5. Anterior socket; 6. Ventral tip of posterior cardinal tooth; 7. Ventral tip of anterior cardinal tooth; 8. Postero-dorsal shell curvature; 9.Antero-dorsal shell curvature; 10.Dorsal tip of adductor/retractor muscle scar; 11. Junction of ventral tip of adductor-retractor muscle scar; 12. Pallial line; 13. Anterior end of the shell; 14.Ventral end of the shell; 15. Posterior end of the shell

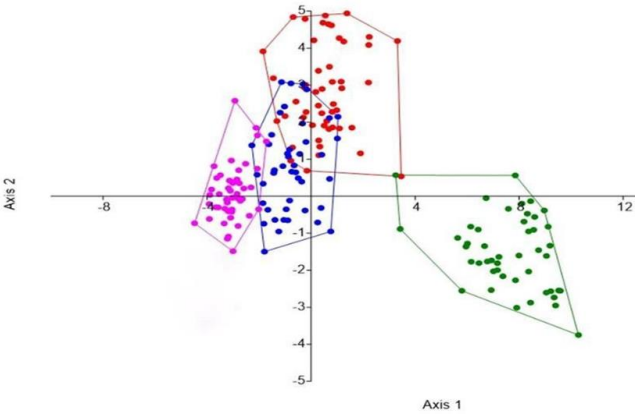

Figure 3. CVA scatter plot of the shape variation of the interior ventral left valves. *Spondylus squamosus* (pink); *S. versicolor* (red); *S. limbatus* (blue) and *S. varius* (green)

The shells of individual specimens of S*podylus* have the same basic morphological types that can be found in all species. The adductor muscle scar and the cardinal area of the hinge made it comparable to other species. In terms of color, these species have diverse marginal color bands. The *S. limbatus* has a deep purple margin band, while the S. versicolor has a deep orange color. The shell color is mainly determined by the presence of pigments produced by the mantle, and its diet may also contribute to coloration. However, their function for the animal is sometimes less clear and has been the focus of many ecological and evolutionary studies (Williams 2016). Several observations have made the evolutionary interpretation of shell color more complex; Grant and Williams (2018) elaborated that conspicuous shell color patterns also exist in mollusks buried in sediment. Saenko and Schilthuizen (2021) revealed that evo-devo studies require the identification of pigments to understand the genetic basis of shell coloration.

The taxonomic and biological literature has been exceedingly disparate in using names for a given species (Lodeiros et al. 2016). Its delinquent taxonomy of the *Spondylus* groups is due to its extreme intraspecific variation. The genus *Spondylus* is commonly distorted in shape because of the crowding of epibionts or because it is attached to the rocky substratum. Some of the bivalve species spent most of their time in semi-infaunal positions and were at risk of being attacked by predators, as observed by drilling marks on the shells (Gordillo and Archuby 2014).

The epibionts attached and cemented on the outer shells make identification and characterization uncertain. Habitat preference and epibionts are some of the factors of hybridization that confound the species' identification (Martonos et al. 2019). This study suggests that the most distinguishable characteristic of the *Spondylus* is the internal shell.

Interior shell patterns

It is clear from the ensuing analysis that the interior shell pattern can be used to classify the *Spondylus* species in Lianga Bay (Eastern Mindanao, Philippines). Aside, it detects variations within the same species. Further analysis of the data using the Multivariate Analysis of Variance (MANOVA) showed significant differences regarding the shell shapes of the five populations of Spondylid species (Wilk's lambda= 0.00188; Pillai trace= 2.902). Overall, the result indicates significant differences in the internal shell characters of sampled Spondylid species (p-value < 0.05).

Table 1. Eigenvalues and percentages of variance for the first three CVs from Canonical Variates Analysis (CVA) for spondylid species

CV	Eigen value	Total variances (%)
1	17.89	72.87
2	3.56	14.53
3	0.74	3.12

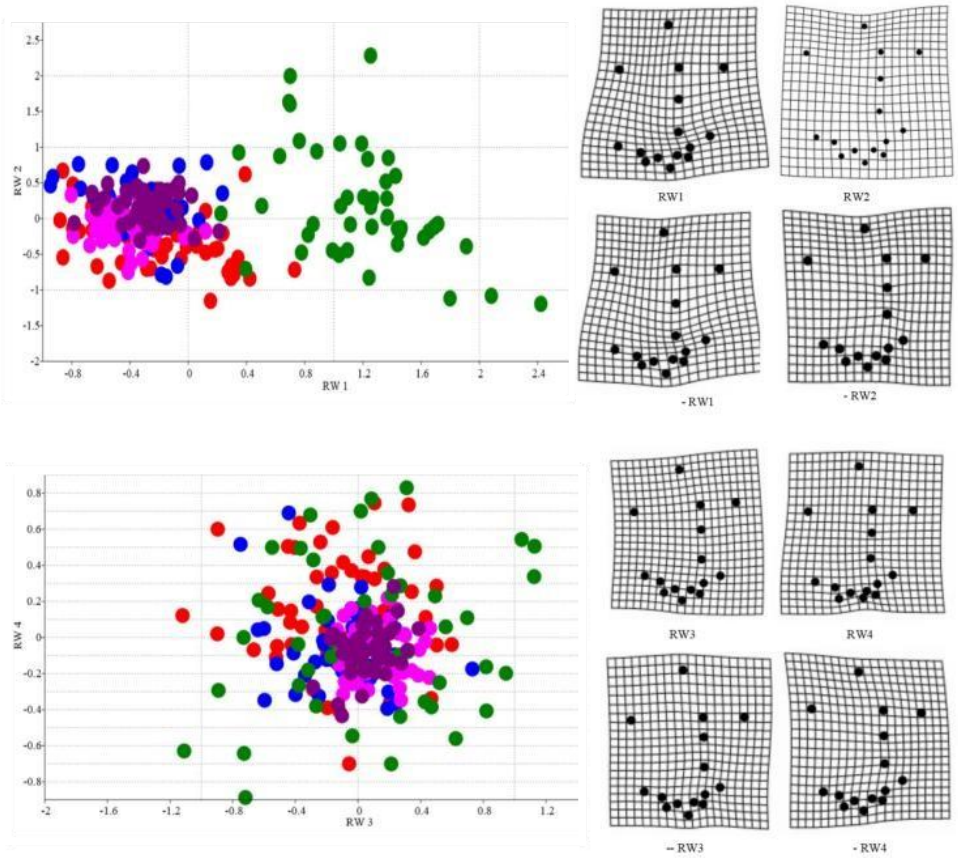

Figure 4. Relative warps analysis showing the first four warps and the associated deformation grids at the approximate minimal and maximal occupied values of the Spondylid species

Therefore, to determine which character may have influenced the classification, the first four (4) relative warps, thin-plate spline images for the approximate minimum and maximum occupied values per warp are presented (Figure 4). The groups/populations of the Spondylid species in RW1 (36.87%), RW2 (19.29%), RW3 (10.27%), and RW4 (7.85%) were best differentiated. Higher percentages indicate that that particular relative warp captures more variation in the morphological characters.

The groups or populations of the Spondylid species were best differentiated using the information captured by RW1, RW2, RW3, and RW4. The relative warps captured the most significant sources of variation in the morphological characters analyzed, leading to effective differentiation between the groups or populations of the species. The RW1 correlates with the shell length as *S. varius* was remarkably distinguished among the groups. The negative values for RW2 indicated the increasing size (length) of the cardinal teeth of the Spondylid species. There was a shorter dorsal tip of the adductor/retractor muscle scar to the junction of the ventral tip of the adductor-retractor muscle scar. There was an increasing size of the palial line down to the ventral tip of the adductor-retractor muscle scar. The RW3 reflected the sizeable cardinal teeth but less pallial line. The low values of RW4 corresponded to the rotation of the cardinal tooth, making it distinctly elongated.

There are basically two factors (environmental/ecological and evolutionary) that explain the wide variation of the Spondylid groups, considering that these species have great morphological similarity; each species has its unique phenotypic variations, often related to its habitat in natural conditions – biotic and abiotic factors (Jijina et al. 2023). The shell species' morphological divergence resulted in phenotypic plasticity and selection associated with the habitat and range of environments, affecting the shell shape and integrity (Proćków et al. 2018). The distinguishable internal shell characteristics of the *Spondylus* compared with other similar specimens on the internal shell are the marginal band, adductor muscle scar, and the cardinal area of the hinge, making it comparable to other species. The two most distinct characteristics among the Spondylid species were the (1) distance of the pallial line towards the ventral tip of the adductor/muscle scar and the (2) size of the cardinal tooth (Figure 4). This study showed that the pallial lines among the species depend on the size and shape of the adductor/muscle scars. In Venerid bivalves, the pallial line is the characteristic that differs among shells (Carboni et al. 2021).

The color of their hinge teeth is inadequate for identification in Spondylid, considering that most specimens had brown hinge teeth. The size of the hinge teeth was considered for identification. The adult hinge plate in adults has two large corral teeth in the right (lower) shell and the corresponding sockets in the left shell. The adductor muscle scar is also the most important character to be established, considering that the abductor muscle scar is mostly in the midline of the shell. A large muscle scar posterior to the center of the shell characterizes it. The adductor muscle scar is mostly posterior to the midline of the shell. Thus, the left valve has the adductor muscle scar mostly to the left of the midline, and the right valve has a scar mostly to the right. The adductor/muscle scars of the species were almost the same in shape but relatively different in size. These internal shell characters could be applied as tentative IDs in the field, considering that the Spondylidae shells have a wide variation range of shape, color, and ornamentation, causing taxonomic frustration (Rocha et al. 2015).

The individual shell character measurements posed some caveats. The growth and shape of bivalves and the degree to which they vary concerning environmental factors have been recorded for several species and habitats (Bergström and Lindegarth 2016; Kroeker et al. 2016). Shell shape differs across the habitat they occupied by the bivalves (Telesca et al. 2018); it depends on the different physical and ecological conditions such as slope, wave energy, and wave exposures. The phenotypic plasticity of the Spondylid groups is possible across the habitats is evident. Bourdeau et al. (2015) defined this type of character as an environmentally contingent expression of phenotypes; they elaborated that the cause of this expression could be adaptive (like the development and behavior in response to environmental cues) and non-adaptive (for example, stressful environments or poor diets result in slow growth, low survival, or low fecundity). In addition, Ruaza and Ilano (2023) detected significant differences in all shell characters across sampling sites, which means the location and habitat preferences may also be a factor. Certain shell characters exhibited differences due to their coping ability with the substrates or their adaptation to varying environmental conditions.

This study provides significant advancement tools in biology and shell research, which serves as baseline data that could help students, researchers, educators, and the general public identify the *Spondylus* species. The novel use of geometric morphometric study as a minimal yet effective tool in *Spondylus* species identification is of great help in realigning previous perceptions of local constituents. Further, the recent study could help the government in its effort to protect and conservation measures for *Spondylus* species in the region.

In conclusion, this study provides additional information and understanding of the morphological variations of the Spondylid species in Lianga Bay, Surigao del Sur, Philippines. The landmark-based geometric morphometry successfully determined the variation in the five Spondylid species. The disparity of their internal shell characters showed significant differences despite their great morphological similarity. The significant differences observed in the internal shell characters among the Spondylid species demonstrate that even small variations can lead to distinct morphological differences. This finding contributes to our knowledge of species differentiation within this group and highlights the importance of considering internal shell characters in taxonomic and ecological studies.

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