



# Differences in sagittal otoliths between two morid species: insights into the genus *Physiculus* (Moridae: Gadiformes)

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*Sagittae* are widely used as tools in taxonomic and ecological studies of fishes, especially when external morphological characters are conserved or ambiguous. We analyzed morphological variation between two congeneric species of *Physiculus*: *P. cirm*, endemic to the Saint Peter and Saint Paul Archipelago, and *P. kaupi*, distributed along the Brazilian continental slope. Fifty adult specimens (25 per species) were examined using qualitative descriptions, morphometrics with shape indices, and 4th and 5th order wavelet contour decomposition. This work represents the first morphometric description and analysis of their sagittal otoliths. Both species exhibited sagitiform otoliths with a plane-convex profile and elliptical *ostium*, but the anterior region is more rounded in *P. cirm* and more peaked in *P. kaupi*, whereas the posterior region is lanceolate to rounded in *P. cirm* but lanceolate in *P. kaupi*. Statistically significant differences were found in otolith height/otolith length (OH/OL), otolith thickness/ otolith length (OT/OL), *sulcus acusticus* area/ otolith area (SA/OA), and otolith length/ total length (OL/TL). Classification using morphometric indices and 5th order wavelets achieved 98% accuracy, highlighting strong discriminative potential. These morphological differences likely reflect both taxonomic divergence and adaptation to deep-sea habitats, supporting otolith morphology for species identification and ecological inference in deep-sea fishes.

**Keywords:** Morphology, Morphometry, Southwestern Atlantic, Wavelets.

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Os *sagittae* são amplamente utilizados como marcadores naturais em estudos taxonômicos e ecológicos de peixes, especialmente quando os caracteres morfológicos externos são conservadores ou ambíguos. Analisamos a variação morfológica entre duas espécies congêneres de *Physiculus*: *P. cirm*, endêmica do Arquipélago de São Pedro e São Paulo, e *P. kaupi*, distribuída ao longo da margem continental brasileira. Cinquenta espécimes adultos (25 por espécie) foram examinados utilizando descrições qualitativas, morfometria com índices de forma, e decomposição de contorno por *wavelets* de 4ª e 5ª ordens. Este trabalho representa a primeira descrição e análise morfométrica de seus otólitos sagitta. Ambas as espécies apresentaram otólitos sagitiformes com perfil plano-convexo e *ostium* elíptico, entretanto a região anterior é mais arredondada em *P. cirm* e mais pontiaguda em *P. kaupi*, enquanto a região posterior é lanceolada e arredondada em *P. cirm*, mas exclusivamente lanceolada em *P. kaupi*. Foram encontradas diferenças estatisticamente significativas nas razões altura/comprimento do otólito (OH/OL), espessura/comprimento do otólito (OT/OL), área do *sulcus acusticus*/área total do otólito (SA/OA) e comprimento do otólito/comprimento total do peixe (OL/TL). A classificação utilizando índices morfométricos e *wavelets* de 5ª ordem alcançou 98% de acurácia, destacando forte potencial discriminativo. Essas diferenças morfológicas provavelmente refletem divergência taxonômica e adaptação a habitats de águas profundas, apoiando o uso da morfologia dos otólitos para identificação de espécies e inferências ecológicas em peixes de águas profundas.

**Palavras-chave:** Atlântico Sudoeste, Morfologia, Morfometria, *Wavelets*.

## INTRODUCTION

The inner ear of teleost fishes, essential for maintaining balance and sensory perception, is composed of three semicircular canals and three otic capsules: the *sacculus*, *lagena*, and *utricle*. Each capsule contains a specific otolith: the *sagitta*, *asteriscus*, and *lapillus*, respectively (Ladich, Popper, 2004; Collin, 2007; Popper, Fay, 2011). These otoliths are metabolically inert structures, forming part of the mechanoreceptor system, primarily composed of aragonite (95%) and a protein matrix (5%), with trace elements (Campana, 2004; Volpedo, Vaz-dos-Santos, 2015; Schulz-Mirbach *et al.*, 2019).

Among the three otolith pairs, *sagittae* are typically the most morphologically diverse and extensively used in various scientific applications (Assis, 2000; Volpedo, Vaz-dos-Santos, 2015). Otolith morphology varies considerably among species and even within the same species, influenced by physiological factors such as growth, sex, gonadal maturation, and diet, as well as by environmental conditions like depth and salinity, which affect biomineralization processes and morphometric patterns (Gagliano, McCormick, 2004; Popper, Fay, 2011; Avigliano *et al.*, 2014). This variability renders *sagittae* valuable tools for species identification (Rossi-Wongtschowski *et al.*, 2014; Moore *et al.*, 2022; Haimovici *et al.*, 2023), population differentiation (Bose *et al.*, 2017; Vaz-dos-Santos *et al.*, 2023; Almeida *et al.*, 2024), and stock assessment (Soeth *et al.*,

2019; Sbiba *et al.*, 2024; Santificetur *et al.*, 2025). Given the taxonomic complexity and broad distribution of many deep-sea fish groups, the interspecific morphological diversity of *sagittae* otoliths has proven particularly useful.

Among the diverse families of deep-sea fishes, Moridae Moreau, 1881, commonly known as “morid cods”, is notable for its richness, comprising 19 genera and 112 valid species (Fricke *et al.*, 2025). Within this family, *Physiculus* Kaup, 1858 is the most species-rich genus. In the Atlantic Ocean, 12 *Physiculus* species have been recorded, four of which occur in Brazilian waters: *P. cirm* Carvalho-Filho & Pires, 2019, endemic to the Saint Peter and Saint Paul Archipelago; *P. fulvus* Bean, 1884, distributed in the northern region; *P. karrerae* Paulin, 1989, occurring along the southeastern and southern coasts; and *P. kaupi* Poey, 1865, which has a broader range extending from the northeastern to the southern Brazilian coast (Paulin, 1989; Oliveira *et al.*, 2015; Pires *et al.*, 2019; Lemes, Melo, 2025).

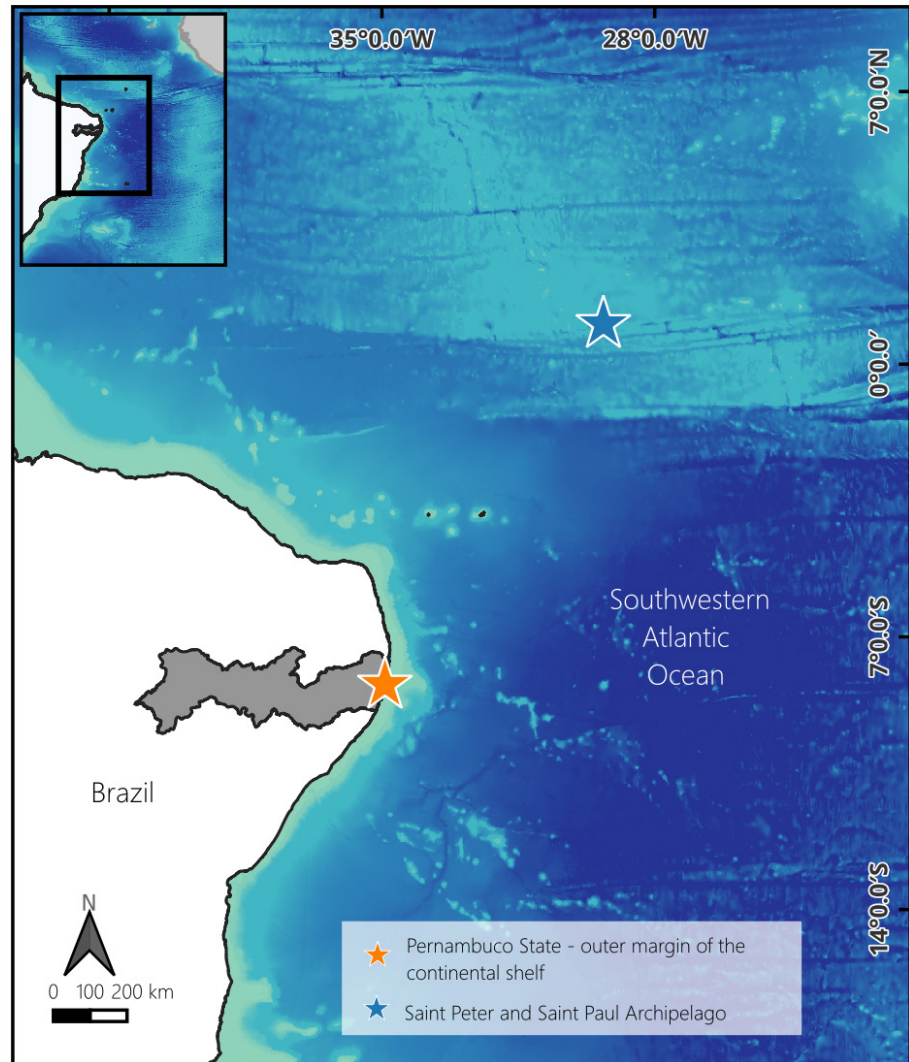
This study aims to distinguish *P. cirm* and *P. kaupi* based on the morphology and morphometry of *sagittae*, including contour analyses using 4<sup>th</sup> and 5<sup>th</sup> order wavelet decomposition. Given the limited knowledge of the genus *Physiculus*, particularly in the South Atlantic, otolith-based approaches represent valuable tools for improving taxonomic resolution, understanding population structure, and supporting fisheries monitoring of deep-sea fish species.

## MATERIAL AND METHODS

**Study area.** This study was conducted concurrently at two sites in the Southwestern Atlantic Ocean (Fig. 1). The first site is located along the outer margin of the continental shelf off the state of Pernambuco (PE; 07°50'S 34°27'W to 08°52'S 34°47'W). This region is characterized by a gently sloping sedimentary surface with a narrow shelf width (Manso *et al.*, 2003). The shelf break lies between 50 and 80 m in depth, followed by a steep upper slope that gradually smooths out beyond 500 m (Kempf, 1970; Araújo *et al.*, 2004; Camargo *et al.*, 2015).

The second site is located around the Saint Peter and Saint Paul Archipelago (SPSPA; 00°55'10"N 29°20'33"W), situated on the equatorial Mid-Atlantic Ridge, approximately 1,060 km off the northeastern coast of Brazil. The archipelago represents the summit of a large sigmoidal submarine ridge rising 3,500 m above the seafloor and comprises five main islets (Belmonte, Southeast, Northeast, Northwest, and South) and five smaller rocks (Campos, 2009).

**Data collection.** A total of 100 *Physiculus* (48 *P. cirm* and 52 *P. kaupi*) specimens were collected through experimental fisheries using bottom-traps, between October 2014 and October 2018, at depths ranging from 200 to 750 m. Immediately after the capture, the specimens were cooled and, as far as possible, labelled at the Fisheries Oceanography Laboratory of Universidade Federal Rural de Pernambuco. The total length (TL, mm) of each fish was measured. Seven specimens were deposited to the Museu de Oceanografia Prof. Petrônio Alves Coelho, Universidade Federal de Pernambuco (two specimens of *Physiculus cirm*: MOCH 1521; five specimens of *Physiculus kaupi*: MOCH 1517). Only mature specimens were recorded in the samples.

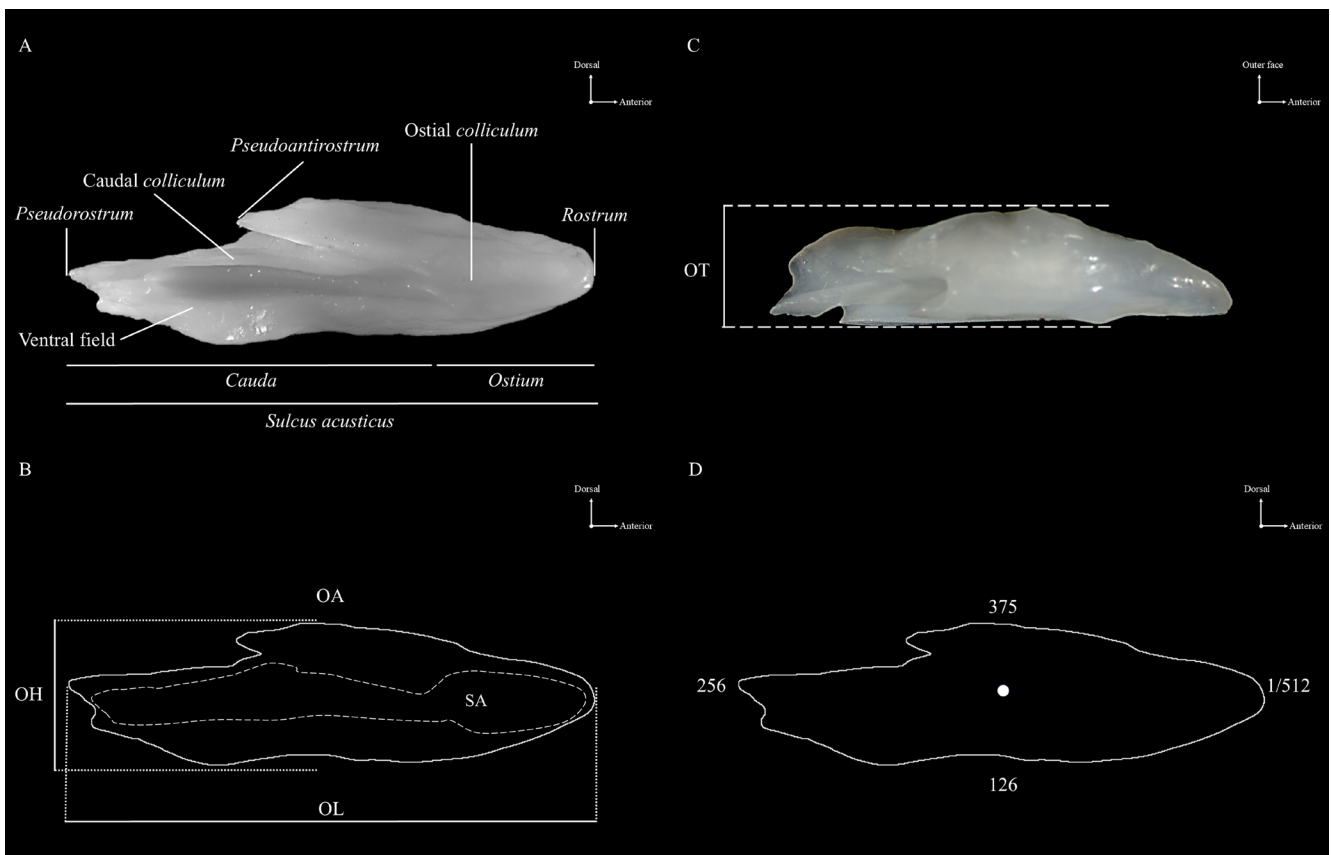


**FIGURE 1** | Map of *Physiculus* sampling locations from the Southwestern Atlantic Ocean. Specimens from *P. kaupi* were collected along the outer margin of the continental shelf off the State of Pernambuco (orange star) and *P. cirm* were collected around the Saint Peter and Saint Paul Archipelago (blue star). Geographic Coordinate System. Datum: Sirgas 2000. Cartographic base: IBGE (2021/2022); SGB (2013); MapasAcademicos (2025); GEBCO (2024).

The *sagittae* were extracted from the ear cavity and washed to remove any remaining macula and vestibule tissue. Images of 25 left and right *sagittae* from each species were taken with the inner face facing upwards and in profile view, using a Zeiss Discovery V12 stereomicroscope with reflected light at 8× magnification. The microscope was equipped with a 5 MP AxioCam MRC5 digital camera, connected via USB. Photographs were taken against a dark background to enhance contrast and facilitate visualization of relevant morphological structures. After the images were captured, left otoliths were used for morphology, morphometry and shape indices, wavelet-based otolith contour decomposition and statistical analysis.

**Morphology.** Morphological analysis of otoliths considered both external and *sulcus acusticus* characteristics. For the external features, the following traits were evaluated: shape, anterior region, posterior region, edges, *rostrum*, *antirostrum*, *pseudorostrum*, *pseudoantirostrum*, and profile. The analysis of the *sulcus acusticus* focused on its position, orientation, opening, morphology, *colliculum*, *ostium*, and *cauda* (Fig. 2A). These morphological characteristics were assessed following the criteria established by Tuset *et al.* (2008) and Rossi-Wongtschowski *et al.* (2014).

**Morphometry and shape indices.** The variables included otolith length (OL, mm), otolith height (OH, mm), otolith thickness (OT, mm), otolith area (OA, mm<sup>2</sup>), and *sulcus acusticus* area (SA, mm<sup>2</sup>) (Figs. 2B–C) (Lombarte, Morales-Nin, 1995; Tuset *et al.*, 2003; Rossi-Wongtschowski *et al.*, 2014). A paired sample *t*-test was used to assess whether there were significant differences between left and right otoliths, based on the mean values of the measured variables. From these measurements, the following morphometric indices were calculated: the ratio of otolith height to otolith length (OH/OL), the ratio of otolith thickness to otolith length (OT/OL), the ratio of *sulcus acusticus* area to otolith area (SA/OA), and the ratio of otolith length to total length of specimen (OL/TL) (Volpedo, Echeverría, 2003; Avigliano *et al.*, 2015; Souza *et al.*, 2019). These indices provide a detailed geometric characterization of the otoliths.



**FIGURE 2 |** External features and otolith morphometry of *Physiculus* species. **A.** Shows the inner face of the left *sagitta* otolith highlighting external anatomical features; **B.** Presents the otolith outline with morphometric measurements including otolith length (OL), otolith height (OH), otolith area (OA, solid line), and *sulcus acusticus* area (SA, dotted line); **C.** Shows the otolith profile indicating its thickness (OT); **D.** Displays the otolith outline with the centroid and selected points along the 512 point digitized contour used for wavelet-based shape analysis.

**Wavelet-based otolith contour decomposition.** The morphological analysis of otolith contours was conducted through wavelet-based signal decomposition, following the methodologies outlined by Parisi-Baradad *et al.* (2010) and Sadighzadeh *et al.* (2014). Wavelet transforms provide a multiscale framework for characterizing local shape variations by decomposing the contour signal into a series of scaled and translated versions of a mother function. The wavelet transform applied follows the general form  $\Psi_s(x) = (1/s)\Psi(\varphi/s)$ , where  $\Psi$  is a compactly supported function,  $\varphi$  denotes a step filter, and  $s$  is a scale parameter controlling frequency and amplitude modulation (Mallat, 1991).

Each otolith was represented by 512 equidistant points extracted along the perimeter, beginning at the rostrum (Fig. 2D). The resulting contour coordinates were processed using wavelet transforms of both 4<sup>th</sup> and 5<sup>th</sup> orders. These specific orders were selected based on their proven sensitivity in capturing fine-scale morphological features, with 5<sup>th</sup> wavelets showing enhanced resolution for detecting subtle variations relevant to stock and population discrimination (Sadighzadeh *et al.*, 2014; Tuset *et al.*, 2015).

Contour extraction and preprocessing were performed using AFORO (<http://aforo.cmima.csic.es>), a dedicated software platform for the acquisition and analysis of otolith morphometric data (Parisi-Baradad *et al.*, 2010). The tool enabled standardized digitization of the contours and facilitated the subsequent application of wavelet-based analytical procedures.

**Statistical analysis.** The nonparametric Mann-Whitney test was used to compare left and right otoliths and between males and females to evaluate bilateral symmetry and sex-related effects on otolith morphology. As no significant differences were found, subsequent analyses were conducted using only left otoliths.

The Mann-Whitney test was also applied to each shape index individually to detect significant morphometric differences among species. Before multivariate analyses, data were mean-centered to eliminate absolute effects and allow for consistent group comparisons (Legendre, Legendre, 1998). For all datasets, including shape indices and wavelet coefficients of 4<sup>th</sup> and 5<sup>th</sup> orders, linear models were used to correct for ontogenetic effects associated with body size. Residuals from these models were used in subsequent analyses (Leonart *et al.*, 2000).

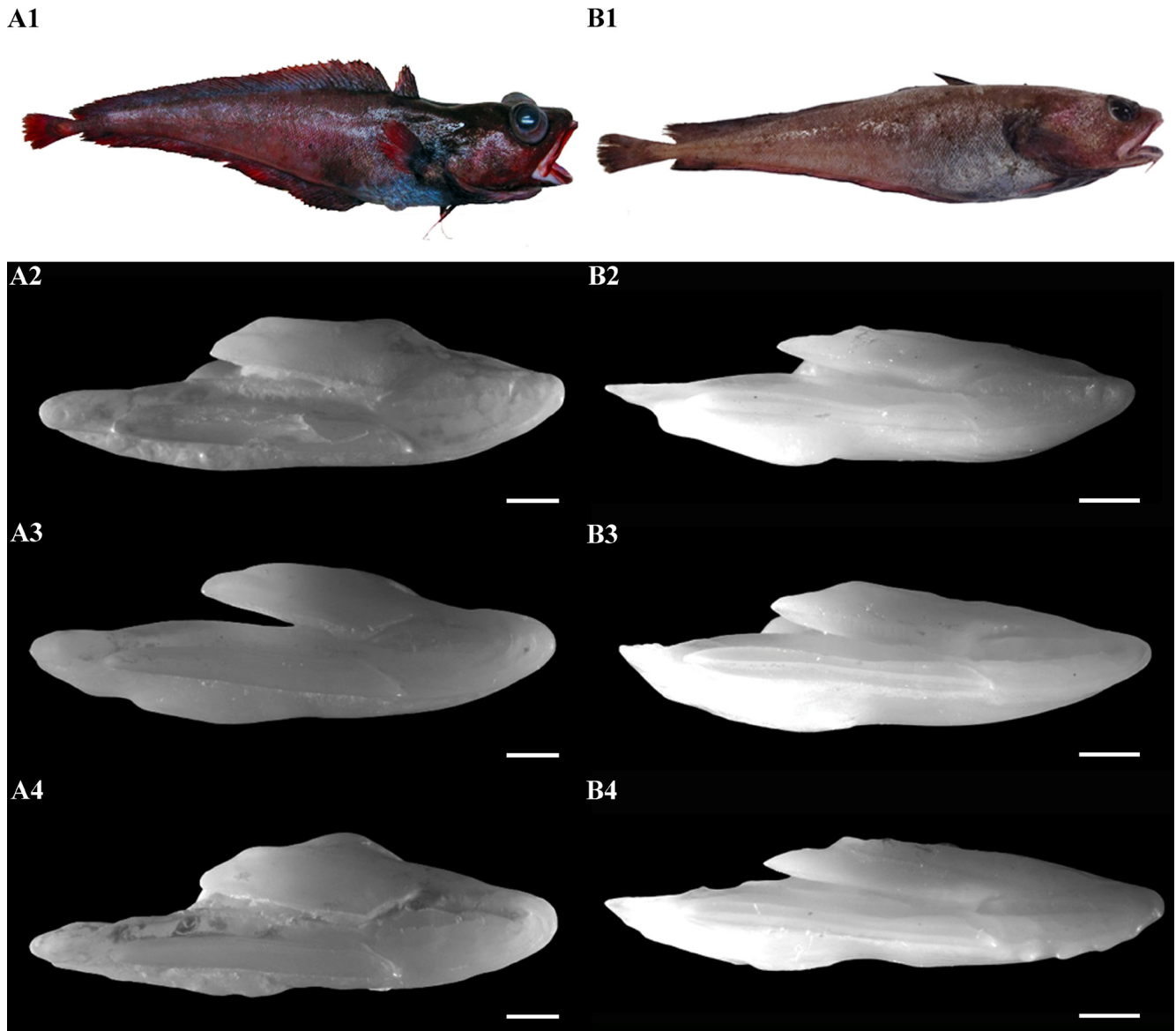
Principal Component Analysis (PCA) was performed on the variance-covariance matrices of each dataset to reduce dimensionality while preserving axes that explain the most variance (Tuset *et al.*, 2015). The calculated morphometric indices for the two *Physiculus* species were subjected to PCA, performed separately for each index.

Principal components (PCs) were retained based on the broken-stick criterion (Gauldie, Crampton, 2002), ensuring that only the most informative variables were included. These PCs were then used as predictor variables in a Linear Discriminant Analysis (LDA) to assess the discriminatory power of otolith morphology for classifying species into their respective trophic guilds (Stransky, MacLellan, 2005). Model performance was validated using both  $k$ -fold cross-validation and the jackknife method, providing robust statistical support and minimizing overfitting risks (Sokal, Rohlf, 1995). The LDA results were evaluated using a confusion matrix, with accuracy calculated.

Finally, differences in otolith morphology among trophic guilds were tested using Permutational Multivariate Analysis of Variance (PERMANOVA), based on Euclidean distances of the adjusted data. All analyses were performed in PAST software v. 4.03 (Hammer *et al.*, 2001).

## RESULTS

**Morphology.** The otoliths of *Physiculus cirm* and *P. kaupi* exhibit considerable morphological similarities, most notably a common sagittiform shape (Fig. 3). Nevertheless, the anterior region is more rounded in *P. cirm* and more peaked in *P. kaupi*, whereas the posterior region is lanceolate to rounded in *P. cirm* and lanceolate in *P. kaupi*. The dorsal margin in *P. cirm* is entire and slightly elevated at the center, while in *P. kaupi* it is entire with uniformly low relief. These characteristics result in a broader and more rounded contour in *P. cirm*, contrasting with the narrower and more peaked contour found in *P. kaupi*. All other morphological characteristics are similar between the two species. The Tab. 1 presents the detailed description of the morphological characteristics of both species.



**FIGURE 3** | Specimen and respective left *sagitta* otoliths of *Physiculus cirm* (A1–A4) and *P. kaupi* (B1–B4), with total length (TL) and otolith length (OL) as follows: A2: 204 mm TL, 10.94 mm OL; A3: 249 mm TL, 11.20 mm OL; A4: 279 mm TL, 12.56 mm OL; B2: 210 mm TL, 9.03 mm OL; B3: 235 mm TL, 10.25 mm OL; B4: TL 274 mm TL, 12.38 mm OL. Scale bars = 1 mm.

**TABLE 1** | Comparative morphological characteristics of the *sagittae* otoliths of *Physiculus cirm* and *P. kaupi*.

Features	<i>Physiculus cirm</i>	<i>Physiculus kaupi</i>
Shape	Sagitiform	Sagitiform
Anterior region	Round to Peaked	Peaked
Posterior region	Round to Lanceolated	Lanceolated
Dorsal edge	Slightly elevated at center	Low relief throughout
Ventral edge	Entire	Entire
Rostrum	Developed	Developed
Antirostrum	Absent	Absent
Pseudorostrum	Developed	Developed
Pseudoantirostrum	Developed	Developed
Profile	Plane-convex	Plane-convex
Sulcus acusticus position	Median	Median
Sulcus acusticus orientation	Horizontal	Horizontal
Sulcus acusticus opening	Caudal	Caudal
Sulcus acusticus morphology	Heterosulcoid	Heterosulcoid
Colliculum	Heteromorphic	Heteromorphic
Ostium	Elliptic	Elliptic
Cauda	Funnel-like	Funnel-like

**Morphometry and shape indices.** Means of the raw measurements and derived shape indices for both *Physiculus cirm* and *P. kaupi* are presented in Tab. 2. Morphological indices OH/OL, OT/OL, SA/OA, and OL/TL were calculated and compared between species. All indices showed statistically significant differences according to the Mann-Whitney U test: OH/OL ( $U = 22$ ;  $p < 0.0001$ ), OT/OL ( $U = 78$ ;  $p < 0.0001$ ), SA/OA ( $U = 68$ ;  $p < 0.0001$ ), and OL/TL ( $U = 109$ ;  $p < 0.0001$ ).

The calculated morphometric indices revealed distinct patterns of morphological variation between species. Four principal components (PCs) were retained; PC1 explained 66% of the variance and PC2 accounted for 17%. A confusion matrix indicated an overall classification accuracy of 98%, with correct classification rates of 100% for *P. cirm* and 96% for *P. kaupi* (Tab. 3A). PERMANOVA analysis applied to the shape indices showed statistically significant differences between species ( $F = 42.23$ ;  $p < 0.0001$ ).

**Wavelet-based otolith contour decomposition.** Mean wavelet coefficients of the 4<sup>th</sup> and 5<sup>th</sup> orders were calculated for the two *Physiculus* species (Fig. 4). Separate Principal Component Analyses (PCA) for each wavelet order revealed distinct morphological variation patterns between the species. For the 4<sup>th</sup> order coefficients, PC1 explained 43% of the total variance and PC2 accounted for 14%. Based on the Broken Stick criterion, 35 principal components were retained for Linear Discriminant Analysis (LDA). The resulting confusion matrix (Tab. 3B) showed an overall classification accuracy of 90%, with correct classification rates of 92% for *P. cirm* and 88% for *P. kaupi*.

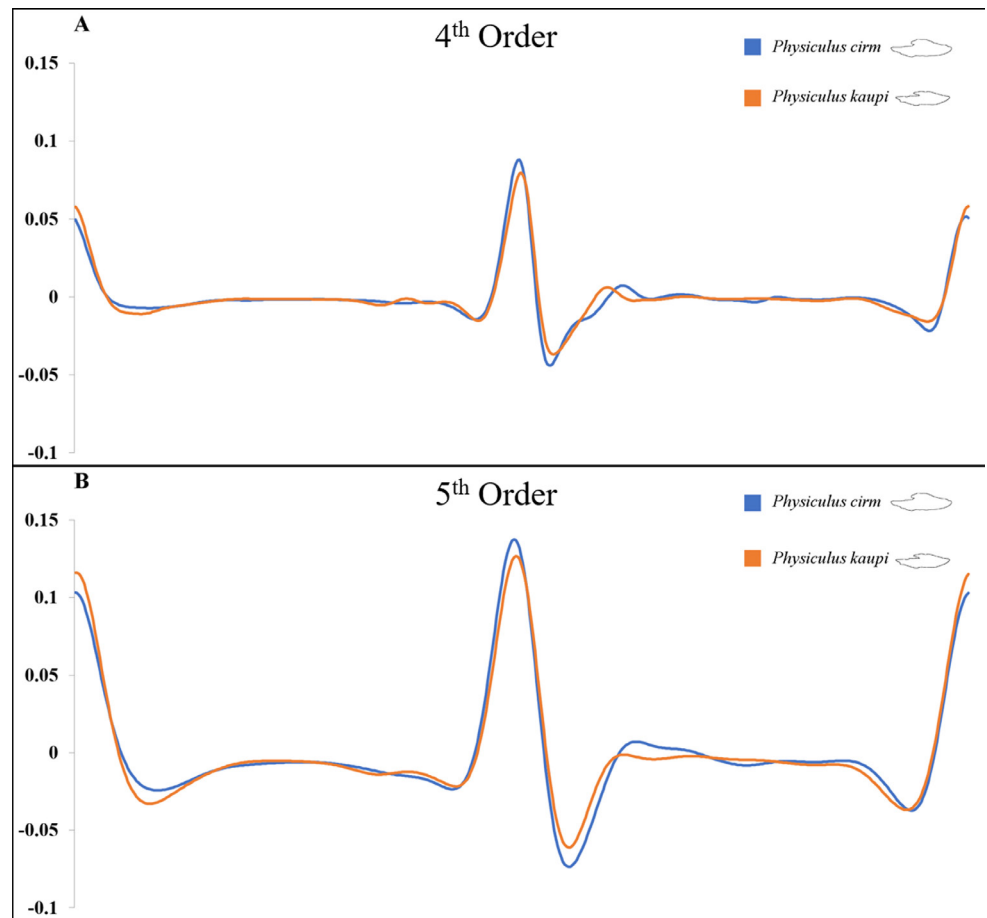
**TABLE 2** | Minimum and maximum values, range of means, and standard deviation (SD) for morphometric variables and shape indices of the left *sagitta* otolith of *Physiculus kaupi* and *P. cirm*. N = number of otolith; TL = fish total length (mm); OL = otolith length (mm); OH = otolith height (mm); OT = otolith thickness (mm); OA = otolith area (mm<sup>2</sup>); SA = *sulcus acusticus* area (mm<sup>2</sup>).

	<i>Physiculus cirm</i>				<i>Physiculus kaupi</i>			
	Min	Max	Mean	SD	Min	Max	Mean	SD
N	25				25			
TL	174	315	253	40	206	274	231	19
OL	9.45	14.43	11.98	1.38	8.02	12.38	9.85	0.95
OH	3.03	4.28	3.7	0.35	2.12	3.02	2.64	0.21
OT	2.9	3.90	3.41	0.40	2.01	3.10	2.35	0.32
OA	18.69	38.54	28.27	5.68	10.5	24.31	16.67	2.72
SA	7.43	15.89	11.66	2.59	3.26	8.14	5.91	0.93
OH/OL	27.56	37.04	31.03	1.87	23.4	29.77	26.85	1.69
OT/OL	23.86	32.91	28.73	2.50	17.8	29.77	24.01	2.94
SA/OA	34.43	45.48	41.1	2.60	29.2	42.96	35.59	3.57
OL/TL	4.21	6.64	4.77	0.52	3.52	4.87	4.27	0.33

**TABLE 3** | Jackknife reclassification matrix for two *Physiculus* species based on different otolith analysis approaches: (A) morphometric indices, (B) 4<sup>th</sup> order wavelet coefficients, and (C) 5<sup>th</sup> order wavelet coefficients. The actual species, *P. cirm* and *P. kaupi*, are listed in rows, while the predicted classifications are shown in columns. The last column (%) indicates the classification accuracy for each species. The overall accuracy for each method is provided in the last row.

Real species	Predicted species		
A	<i>Physiculus cirm</i>	<i>Physiculus kaupi</i>	%
<i>Physiculus cirm</i>	25	0	100
<i>Physiculus kaupi</i>	1	24	96
Total	26	24	98
B	<i>Physiculus cirm</i>	<i>Physiculus kaupi</i>	%
<i>Physiculus cirm</i>	23	2	92
<i>Physiculus kaupi</i>	3	22	88
Total	26	24	90
C	<i>Physiculus cirm</i>	<i>Physiculus kaupi</i>	%
<i>Physiculus cirm</i>	25	0	100
<i>Physiculus kaupi</i>	1	24	96
Total	26	24	98

In contrast, PCA on the 5<sup>th</sup> order coefficients revealed that PC1 explained 32% and PC2 19% of the variance. Forty-four components were retained for LDA, which achieved an overall classification accuracy of 98% (Tab. 3C), with *P. cirm* correctly classified in 100% of cases and *P. kaupi* in 96%.



**FIGURE 4 |** The graphs illustrate the average shape variation captured by the 4<sup>th</sup> order (A) and 5<sup>th</sup> order (B) wavelet transformations for *Physiculus cirm* (blue line) and *P. kaupi* (orange line). The lines represent each species mean wavelet decomposition patterns of otolith contours.

PERMANOVA analysis applied to the wavelet coefficients of both orders detected statistically significant differences between the species, with greater differentiation for the 5<sup>th</sup> order coefficients ( $F = 3.533$ ,  $p = 0.0073$  for 4<sup>th</sup> order;  $F = 5.257$ ,  $p < 0.0001$  for 5<sup>th</sup> order).

## DISCUSSION

The family Moridae can be subdivided into three main morphological groups based on otolith characteristics: *Mora* group, *Pseudophyscis* group, and *Physiculus* group (Karrer, 1971; Fitch, Barker, 1972; Schwarzhans, 2019). The *Physiculus* group, which includes the species analyzed in this study, comprises the genera *Gadella* Lowe, 1843; *Laemonema* Günther, 1862; *Momonatira* Paulin, 1986; *Paralaemonema* Trunov, 1990; *Physiculus*, *Salilota* Günther, 1887; and *Tripteroophyscis* Boulenger, 1902 (Schwarzhans, 2019).

Otoliths in this group are characterized by being thick and elongated, with a plane-convex profile, a flat inner face, and a *sulcus acusticus* extends over the entire inner face,

with a short, elliptical *ostium*. In contrast, otoliths from the *Mora* and *Pseudophyscis* groups tend to be less compact, thinner, and exhibit more pronounced internal curvatures (Schwarzahns, 2019).

Both *P. cirm* and *P. kaupi* conform to the general otolith pattern of the *Physiculus* group, displaying robust *sagittae* with a plane-convex profile and a short, elliptical *sulcus acusticus*. However, notable morphological differences exist between the two species. *Physiculus kaupi* exhibits more elongated otoliths, with an OH/OL ratio of  $26.85 \pm 1.69$  compared to  $31.03 \pm 1.87$  in *P. cirm*. Schwarzahns (2019) listed *P. kaupi* among the species for which otoliths are not known. However, based on the characteristics observed in the present study, this species can be assigned to a cluster of very slender otoliths, characterized by low dorsal rims and occasional posteroventral expansions on the outer face. Species such as *P. cyanostrophus* Anderson, Tweddle, 2002; *P. dalwigki* Kaup, 1858; *P. fulvus*; *P. grinnelli* Jordan & Jordan, 1922; *P. japonicus* Hilgendorf, 1879; *P. longicavis* Parin, 1984; *P. microbarbata* Paulin & Matallanas, 1990; and *P. nigripinnis* Okamura, 1982 share this morphology and are widely distributed in tropical and subtropical regions of the Pacific and Indian Oceans.

Furthermore, based on the otolith characteristics observed in the present study, *P. cirm*, a species described by Pires *et al.* in 2019 and thus not previously analysed, can be assigned to the second morphological category proposed by Schwarzahns also in 2019, defined by moderately elongated otoliths with a slight expansion of the mid-dorsal rim, a broad concavity in the antero-dorsal region, and a subtly upward-curving *ostium*. Members of this assemblage include *P. karrerae*; *P. luminosa* Paulin, 1983; *P. natalensis* Gilchrist, 1922; *P. nigrescens* Smith & Radcliffe, 1912; and *P. therosideros* Paulin, 1987; which mainly inhabit tropical to temperate waters of the Atlantic and Indian Oceans.

A third distinct group described by Schwarzahns (2019) exhibits more compressed otoliths featuring pronounced mid-dorsal expansions and, occasionally, an additional post-dorsal extension on the outer face. This assemblage comprises species such as *P. argyropastus* Alcock, 1894; *P. capensis* Gilchrist, 1922; *P. cynodon* Sazonov, 1986; *P. huloti* Poll, 1953; *P. marisrubri* Brüss, 1986; *P. nematopus* Gilbert, 1890; *P. rastrelliger* Gilbert, 1890; and *P. roseus* Alcock, 1891; distributed across the Eastern Pacific, Southwestern Pacific, Indian Ocean, and Southwestern Atlantic. These differences illustrate the morphological diversity within the *Physiculus* group and highlight the value of otoliths as tools for both taxonomic and potentially ecological differentiation.

In Brazil, the only Moridae species with previously described otolith morphology are *Gadella imberbis* (Vaillant, 1888) and *Laemonema goodebeanorum* Meléndez & Markle, 1997 (Rossi-Wongtschowski *et al.*, 2014). Both species exhibit typical features of the *Physiculus* group, such as a sagittiform shape, prominent *pseudorostrum* and *pseudoantirostrum* development, and a heterosulcoid *sulcus acusticus* with caudal opening. They also share a plane-convex profile and pronounced otolith thickness, distinguishing Moridae from other teleost families.

In addition to these morphological differences, both *P. cirm* and *P. kaupi* possess relatively large size of their *sagittae* (OL/TL). According to Paxton (2000), otoliths with OL/TL ratios above approximately 4–5% of standard length are considered large, a characteristic often observed in deep-water and luminous fish species, where enhanced auditory capabilities are beneficial. This trait aligns with patterns described for deep-sea fishes, where enlarged otoliths are often linked to an enhanced role of auditory

perception and acoustic communication in low-light environments (Platt, Popper, 1981; Popper, Fay, 1993; Paxton, 2000). As suggested by Gauldie (1988) and Lychakov, Rebane (2000), otolith size can indicate the functional capacity of the teleost inner ear, particularly in relation to sound transduction efficiency. In deep-sea habitats, where visual cues are limited and ambient noise is low, larger otoliths may serve as functional adaptations that improve the detection of sound or vibration stimuli (Paxton, 2000; Lombarte *et al.*, 2010).

Moreover, although environmental factors such as temperature and depth influence otolith development (Simkiss, 1974; Morales-Nin, 1987), they do not fully explain the magnitude of variation observed among species inhabiting similar bathymetric zones. This suggests that, beyond environmental influences, intrinsic factors such as evolutionary history and functional specialization play a key role in shaping otolith size (Lombarte, Leonart, 1993; Losos, Miles, 1994). Thus, the shared otolithic features of *P. cirm* and *P. kaupi* reflect not only a phylogenetic link within the *Physiculus* group but also possible adaptive convergence related to the sensory demands of deep-sea environments.

The OH/OL and OT/OL ratios showed differences between the species analyzed, suggesting subtle yet consistent variations in otolith robustness. *Physiculus cirm* tends to exhibit proportionally taller and thicker otoliths compared to *P. kaupi*, which may reflect functional differences related to postural stability, vibration detection, and habitat use. According to Tuset *et al.* (2003), the OH/OL ratio is one of the most effective shape descriptors for species discrimination, reflecting both phylogenetic constraints and ecological adaptations. Volpedo, Echeverría (2003) noted that taller and thicker otoliths are often associated with species of lower mobility, which rely more heavily on equilibrium and positional perception. Lombarte *et al.* (2010) further emphasized that environmental and functional factors, such as depth, swimming behavior, and vertical position in the water column, shape these otolith features. Therefore, although the differences between the species are not pronounced in isolation, the combined morphometric patterns contribute to the distinction between *P. cirm* and *P. kaupi*, suggesting also a slight divergence in their sensory and ecological adaptations.

The ratio between the area of the *sulcus acusticus* and the total otolith area (SA/OA) has been widely used as a functional indicator of auditory sensitivity in teleost fishes (Gauldie, 1988; Lombarte, 1992; Arellano *et al.*, 1995). Morphological variations of the *sulcus acusticus* among species reflect ecological differences, indicating adaptations to distinct habitats and behaviors (Lombarte, Popper, 2004; Taylor *et al.*, 2020; Verocai *et al.*, 2023). An increase in this ratio suggests a greater capacity to detect acoustic stimuli, which is associated with higher vertical activity, acoustically complex environments, or increased reliance on hearing over vision (Rogers, Cox, 1988; Aguirre, Lombarte, 1999). In the present study, *Physiculus cirm* exhibited a significantly higher SA/OA ratio than *P. kaupi*, indicating possible auditory specialization related to different habitat use patterns and trophic strategies.

Finally, the analysis of otolith morphology using wavelet transforms proved to be an effective tool for distinguishing *P. cirm* and *P. kaupi*. Although both 4<sup>th</sup> and 5<sup>th</sup> order wavelet decompositions captured relevant morphological variation, the 5<sup>th</sup> order decomposition demonstrated higher classification accuracy, standing out for its greater discriminatory power, similar to what was observed in coastal species (Carvalho *et al.*,

2024). These results highlight the potential of high-resolution contour analysis for identifying morphologically similar taxa. The integration of traditional shape indices with wavelet-based approaches thus represents a robust and complementary strategy for taxonomic and morpho-functional studies (Sadighzadeh *et al.*, 2014; Tuset *et al.*, 2021; Charnpila *et al.*, 2024). Future research should incorporate ontogenetic, genetic, and otolith microchemical data to further elucidate the evolutionary and ecological drivers of *sagitta* morphology.

The results of this study provide the first morphometric description and analysis of its sagittal otoliths and demonstrate that *Physiculus cirm* and *P. kaupi* can be reliably distinguished based on multiple otolith morphological features. Qualitative differences in the anterior and posterior regions, significant variation in shape indices, and distinct contours captured by 4<sup>th</sup> and 5<sup>th</sup> order wavelets consistently support the morphological separation between these two species. The significant differences in OH/OL and OT/OL ratios indicate variations in otolith morphology and robustness between the species. Additionally, the significantly higher SA/OA ratio in *P. cirm* suggests a difference in the relative size of the sensory area. These morphological disparities reflect taxonomic divergence and may be associated with distinct functional adaptations to their deep-sea habitats.

Both species conform to the general otolith morphology of the *Physiculus* group, which is characterized by thick, plane-convex *sagittae* with a short *sulcus acusticus* and elliptical *ostium*. However, consistent interspecific differences, especially those captured by 5<sup>th</sup> order wavelet decomposition, allowed for high classification accuracy. This reinforces the value of high-resolution contour analysis as a powerful tool for distinguishing morphologically conservative taxa. In this context, *sagittae* of *Physiculus* species emerge not only as taxonomic markers but also as integrative structures that encapsulate functional and ecological information, offering a robust framework for systematics, evolutionary inference, and biodiversity assessment in deep-sea environments.

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**César Santificetur:** Conceptualization, Formal analysis, Investigation, Methodology, Writing–original draft, Writing–review and editing.

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**Sara de Castro Loebens:** Data curation, Investigation, Writing–review and editing.

**Alessandra Maria Advíncula Pires:** Data curation, Visualization, Writing–review and editing.

**Danielle de Lima Viana:** Project administration, Writing–review and editing.

**Paulo Guilherme Vasconcelos de Oliveira:** Funding acquisition, Supervision, Writing–review and editing.

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**DATA AVAILABILITY STATEMENT**

The data supporting the findings of this study are available from the corresponding author upon reasonable request.

**AI STATEMENT**

The authors did not use any AI-assisted technologies in the creation of this manuscript or its figures.

**COMPETING INTERESTS**

The authors declare no competing interests.

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