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RESEARCH PAPER

Unveiling otolith shape variation: geometric morphometric analysis of three croaker species (Acanthuriformes: Sciaenidae)

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Abstract

In this study, we employed landmark-based geometric morphometric analysis (GMA) of otoliths in 2D to examine inter-species variations within the genus *Johnius* of the family Sciaenidae collected from the Gopalpur coast of Odisha, India. Our objective was to determine whether otolith shape variation aligns with their morphological uniqueness. A total of 71 left-side otoliths with 14 designated landmarks were considered for GMA. We conducted Principal Component Analysis (PCA), Discriminant Function Analysis (DFA), and Canonical Variate Analysis (CVA) to assess shape variations among *Johnius macrorhynus*, *Johnius dussumieri*, and *Johnius carutta*. Our findings indicate significant shape variation ($p < 0.05$) among these species' otoliths, consistent with their taxonomic distinctiveness. In conclusion, this study highlights the potential of otolith-based geometric morphometric analysis to enhance taxonomic identification and inform future research on fish diversity and evolutionary dynamics.

Keywords Drums · Otolith · CVA · DFA · Shape uniqueness · Species discrimination

Introduction

The Sciaenidae family, commonly known as drums or croakers, is indeed one of the most diverse family within the order Acanthuriformes. It comprises 298 species organized into 68 genera (Chao et al. 2015; Fricke et al. 2024). They are characterized by their ability to produce sound using specialized muscles attached to their swim bladder (Lal Mohan 1984). The structural variations in the swim bladder provide essential morphological markers that aid in generic identification across the diverse family (Sasaki 2001). The family holds significant commercial value in India, underscored by their popularity in both local and international markets, which makes them a vital resource for the fishing industry and coastal communities (Rahangdale et al. 2022; Roul et al. 2022). A total of 38 species in 18 genera have been documented from India (Kosygin et al. 2024). In Odisha, sciaenids are acknowledged as a key group of commercially important demersal fish, comprising a total of 26 species across 13 genera. The genus *Johnius* Bloch, 1793, stands out as the most dominant, featuring 11 species found in the waters of Odisha (Barman et al. 2007; Puvala et al. 2023).

The family is classified mainly by means of morphological characteristics, including the snout, mental pores, barbels, otoliths, and gas bladders. A deep notch between the dorsal spine and soft rays, a lateral line that extends to the caudal fin tip, a somewhat elongated and compressed body, and a unique dental arrangement are some of the important characteristics (Talwar 1995; Hanafi et al. 2023). While these features assist in distinguishing species, some morphological traits can be difficult to differentiate. Due to the overlapping of external morphological features, it is difficult to identify, which often leads to misidentification (Griffiths and Heemstra 1995).

Traditional morphometrics relies on linear measurements such as length, width, and height, which are closely linked

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to size. Consequently, measurements from two different sources may yield similar outcomes, whereas measurements from the same source can produce varying results, significantly complicating shape analysis (Seth et al. 2019). To overcome this, landmark-based geometric morphometrics analysis (GMA) has been used to study the shape variation between different organisms (Adams et al. 2004). The geometric morphometric method uses specific landmarks to explore the morpho space of objects. This approach provides graphical representations of shape differences which are visually appealing and informative. It offers numerous advantages over traditional taxonomic methods. Moreover, analysing shape variation using geometric morphometrics can reveal phenotypic, ecological, and behavioural differences helping to trace the course of evolution (Klingenberg et al. 2003; O'Reilly and Horn 2004). It is also used for predicting inter-specific and intra-specific variation as well (Lorenz et al. 2017).

Otoliths are small calcified structures present in the otic capsule of the head. It is made up of 0.2−10% organic matter in the form of Otolin protein, and calcium carbonate in the form of aragonite (Campana 1999). All bony fish (Teleostei) possess three pairs of otoliths: the Sagitta, Asteriscus, and Lapillus (Campana and Neilson 1985). Sagitta, the largest otolith, undergoes significant morphological changes across species depending on the habitat of the species. The sagittal morphology is species-specific, and most species can be identified by studying some discrete features of sagittal morphology (Hunt 1992; Harvey et al. 2000). Sciaenids are known for their large otoliths, but yet information regarding otolith morphology in these species is limited (Kumar et al. 2012). Otolith analysis plays valuable roles in determining fish age (Karlou-Riga 2000), stock identification (Poulet et al. 2004), and eco-morphological studies (Volpedo and Echeverría 2003), as well as for identifying species in archaeological and fossil records (Carpenter et al. 2003; Jawad et al. 2011). Additionally, otoliths found in the stomach contents of predators provide insights into their diet (Waessle et al. 2003; Kumar et al. 2012).

Otoliths hold significant value in various fields of aquatic research due to their unique properties. They grow incrementally, similar to tree rings, enabling scientists to determine the age of a fish accurately. The composition of otoliths provides insights into the environmental conditions experienced by the fish, as trace elements and isotopes incorporated during growth reflect the water chemistry of their habitat. This allows researchers to infer details about migration patterns and population structure, revealing movement between freshwater and marine environments or different geographic areas (Volpedo and Echeverría 2003; Rodriguez-Mendoza 2006).

We used landmark-based geometric morphometric analysis (GMA) of otoliths in 2D to investigate inter-species variation among three *Johnius* species (Sciaenidae) from the Gopalpur coast, Odisha, India. We aimed to assess whether otolith shape differences reflect their distinct morphological characteristics.

Materials and methods

Sampling

The fish samples were collected from August 2023 to February 2024. A total of 265 sciaenid fish samples were collected through random sampling from the fish landing centres at Boxipalli (19° 14′ 50.06″ N; 84° 53′ 49.84″ E) and Arjyapalli (19° 18′ 24.17″ N; 84° 57′ 47.91″ E), along the Gopalpur coast, Odisha, India with the assistance of local fishermen. Fish samples were initially photographed and then tagged. Using a digital caliper (± 0.1 mm accuracy), the total length (TL), standard length (SL) and head length (HL) of each individual fishes as well as the otolith length (OL), its width (OW) and height (OH) were measured prior to preservation in 10% formalin solution. All the specimens were identified based on the characters provided in the literature (Talwar and Jhingran 1991; Talwar 1995; Sasaki 2001). The fish specimens were identified to be *Johnius amblycephalus* (Bleeker, 1855) ($n = 2$); *J. carutta* Bloch, 1793 ($n = 51$); *J. coitor* (Hamilton, 1822) ($n = 4$); *J. dorsalis* (Peters, 1855) ($n = 5$); *J. dussumieri* (Cuvier, 1830) ($n = 50$); *J. macrorhynus* (Lal Mohan, 1976) ($n = 13$); *Kathala axillaris* (Cuvier, 1830) ($n = 50$), *Nibea maculata* (Bloch & Schneider, 1801) ($n = 14$); *Otolithes ruber* (Bloch & Schneider, 1801) ($n = 17$); and *Pennahia aneus* (Bloch, 1793) ($n = 59$). The most diverse group of species was discovered to be in the genus *Johnius*. We obtained one species from each genus, except for *Johnius*, where six distinct species were identified. All the genera are found to be morphologically distinct from each other, making it relatively easy to identify fish up to the genus level. However, identifying individual species of the genus *Johnius* becomes more difficult due to overlapping morphological characteristics. Thus, GMA of the otolith of individuals of this genus was taken into consideration. Due to the insufficient number of specimens of *J. amblycephalus*, *J. coitor* and *J. dorsalis*, we have excluded them from the analysis and focused only on the rest three species to carry out the study.

Otolith analysis

The tympanic region of each specimen (from deceased fish) was dissected to extract the bony otoliths using fine forceps. Otolith extraction followed the vertical cut procedure of Javadzadeh et al. (2016), with subsequent cleaning and drying following Milton and Chenery (1998). The left sagittal otoliths of each specimen were individually stored in labelled vials. High-quality photographs of the left otolith of each sample were captured using a Leica S9i stereo-zoom microscope, with a 2 mm scale for standardization. During the study 71 numbers of photographs of otoliths belonging to 3 species viz., *J. carutta* ($n=28$); *J. dussumieri* ($n=33$); and *J. macrorhynus* ($n=10$) were selected for geometric morphometric analysis (Fig. 1). The damaged otoliths were excluded from the analysis to prevent error. The program tpsUtil32 (Rohlf 2015) was utilized to generate the tps files from 2D images. A total of 14 landmarks were designated following the protocol outlined by Santos et al. (2022) and Verocai et al. (2023) for the GMA, including: LM1: tip of anterior of the otolith, LM2: pre-ventral angle, LM3, LM5, LM7 and LM11: semi landmarks, LM4: pre-ventral spine, LM6: mid ventral notch, LM8: post-ventral notch, LM9: post dorsal spine, LM10: post dorsal notch, LM12: mid-dorsal notch, LM13: pre-dorsal spine and LM14: dorsal margin (Fig. 2). These landmarks were marked on each specimen using the software tpsDig2.32 (Rohlf 2006). To assess shape variations among the three species, Principal Component Analysis (PCA) (Pearson 1901); Canonical Variate Analysis (CVA) (Fisher 1936), and Discriminant Function Analysis (DFA) were performed using Morpho J software (Klingenberg 2011).

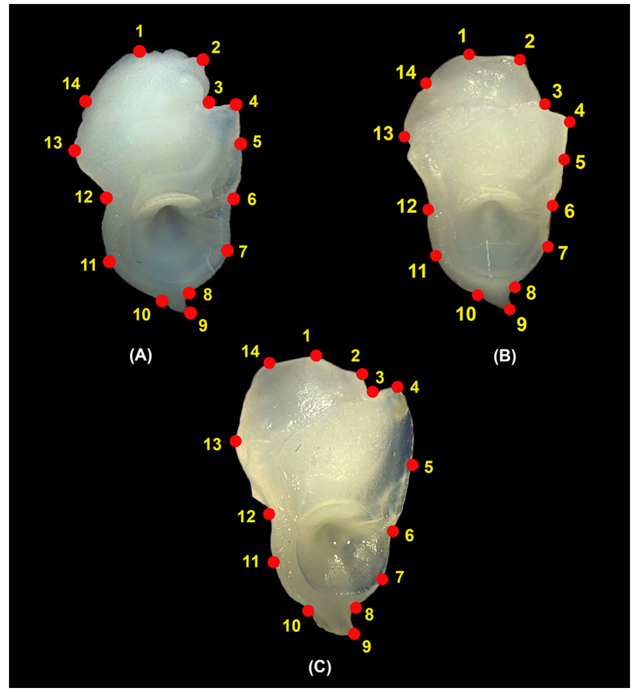

Fig. 2 Different landmarking designated on the ventral side of the left otolith **A** *Johnius macrorhynus* (Lal Mohan, 1976); **B** *J. dussumieri* (Cuvier, 1830); **C** *J. carutta* Bloch, 1793

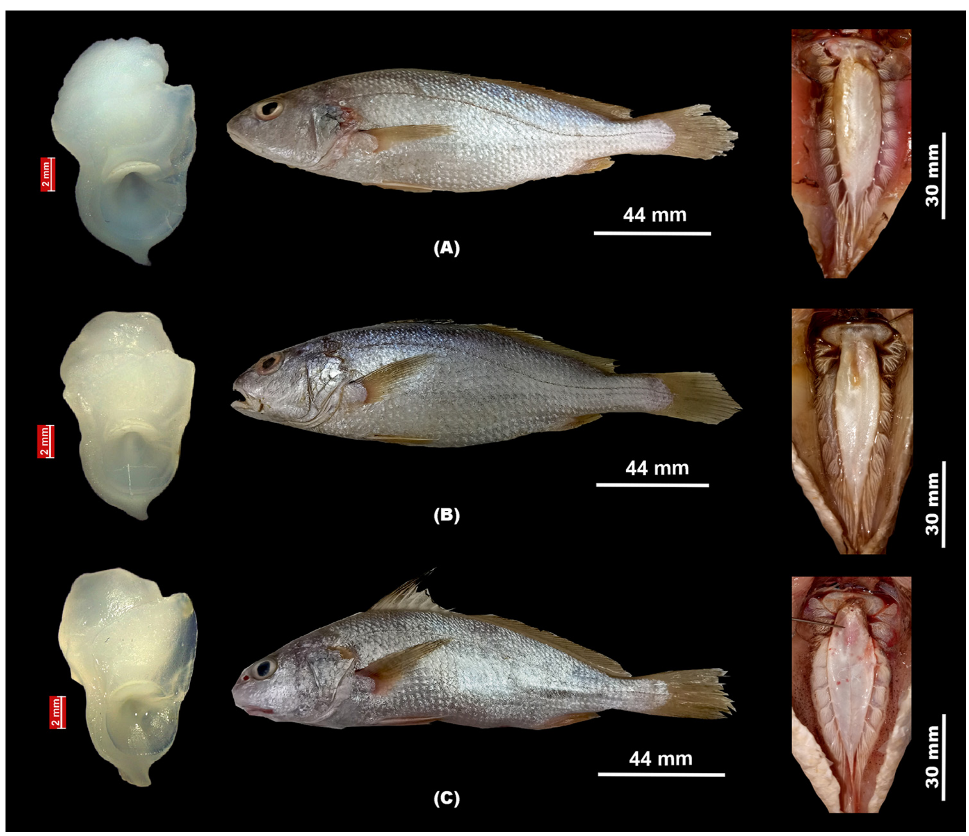

Fig. 1 Lateral view of different Sciaenid species along with their respective left otoliths and swim bladders: **A** *Johnius macrorhynus* (Lal Mohan, 1976); **B** *J. dussumieri* (Cuvier, 1830); **C** *J. carutta* Bloch, 1793

Results

Johnius macrorhynus (Lal Mohan, 1976)

The mean length, width and height of the otolith are 9.42 mm (8.63−10.29), 4.17 mm (3.76−4.69) and 5.88 mm (5.45−6.31) respectively. Procrustes sum of squares is 0.052. Tangent sum of squares is 0.051. Total variance is 0.005. Major variation is found in LM4 and LM13. LM2, LM6, LM10, LM11 and LM12 show very less variation. Moderate variation is found LM1, LM3, LM5, LM7, LM8 and LM9 (Fig. 3A).

Johnius dussumieri (Cuvier, 1830)

The mean length, width and height of the otolith is 6.86 mm (5.07−8.21), 3.29 mm (2.39−4.22) and 4.41 mm (3.33−5.01) respectively. Procrustes sum of squares is 0.236. Tangent sum of squares is 0.234. Total variance is 0.007. In this species, more variation is found at LM 1, LM 3 and LM14. Very less variations are found in LM2, LM6, LM7, LM8. LM9, LM11 and LM13. The landmarks LM4, LM5, LM10 and LM12 show moderate variation (Fig. 3B).

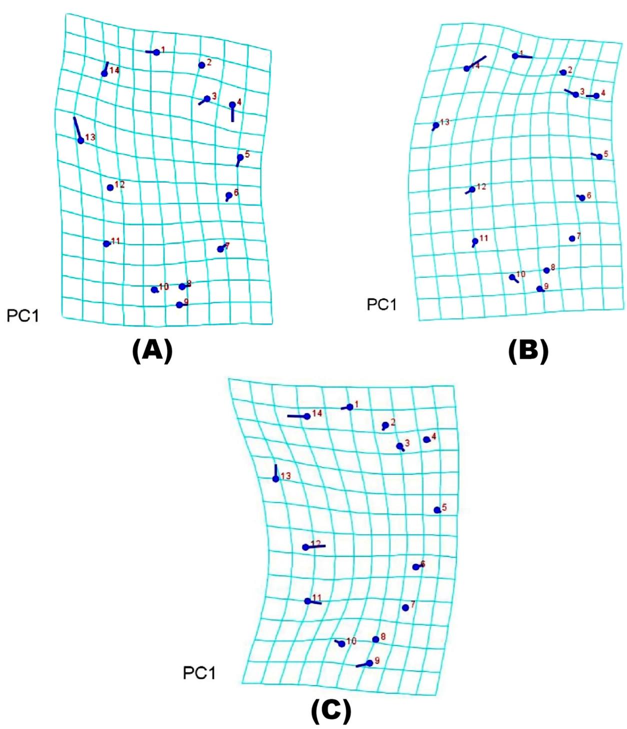

Fig. 3 Lollipop grid transformation of three species. **A** *Johnius macrorhynus* (Lal Mohan, 1976); **B** *J. dussumieri* (Cuvier, 1830); **C** *J. carutta* Bloch, 1793

Johnius carutta Bloch, 1793

The mean length, width and height of the otolith is 8.50 mm (7.76−8.93), 3.37 mm (2.96−3.67) and 5.3 mm (4.83−5.48) respectively. Procrustes sum of squares is 0.126. Tangent sums of squares: 0.125. The Total variance is 0.004. In this species, more variation is found at LM 9, LM11, LM12, LM13 and LM14. Very less variation is found in landmarks LM2, LM4 and LM5. While, LM7, LM3. LM8, LM6 and LM10 show moderate variation (Fig. 3C).

Principal component analysis (PCA)

When all the landmarks of the otoliths of three distinct *Johnius* species are pooled together, the overall Procrustes sum of squares and the tangent sum of squares are 0.58339 and 0.57742, respectively. Principal Component Analysis (PCA) retained 24 PCs. PC1 and PC2 were selected for analysis. The eigen value for PC1 is 0.002262, accounting for 27.426% of the variance, while the eigen value of PC 2 is 0.001675 and the variance is 20.316%.

Canonical variance analysis (CVA)

The first two Canonical variates (CV1 and CV2) were considered for analysis as CV1 had an eigen value of 7.72, accounting for 65.97% of the total variance, while CV2 had an eigen value of 3.98, representing 34.02% of the variance. The Mahalanobis distance between *J. carutta* and *J. macrorhynus* is highest (8.01) and lowest between *J. carutta* and *J. dussumieri* (5.23). P-values from permutation tests (10000 permutation rounds) for Mahalanobis distances among the groups are significant ($p < 0.05$). The Procrustes distance between *J. dussumieri* and *J. macrorhynus* is lowest (0.082) and that of *J. carutta* and *J. macrorhynus* is highest (0.1). There is significant variation in Procrustes distance among all three species (Table 1). A scatter plot of CVA comparing CV1 and CV2 across 71 samples shows a clear separation of the three clusters (Fig. 4).

Discriminant function analysis (DFA)

The Discriminant Function Analysis shows variation among the three species (Table 2). The discriminant scores of *J. carutta* are significantly different ($p < 0.05$ at 95% significance level) with *J. dussumieri* and *J.*

Table 1 Mahalanobis and Procrustes distances among groups of species considered in the analysis

Name of the species	*J. carutta*				*J. dussumieri*			
	Mahalanobis distance	P-values for Mahalanobis distance	Procrustes distance	P-values for Procrustes distance	Mahalanobis distance	P-values for Mahalanobis distance	Procrustes distance	P-values for Procrustes distance
J. dussumieri	5.2370	< 0.0001	0.0841	< 0.0001	–	–	–	–
J. macrorhynus	8.0160	< 0.0001	0.1006	< 0.0001	6.3185	< 0.0001	0.0821	< 0.0001

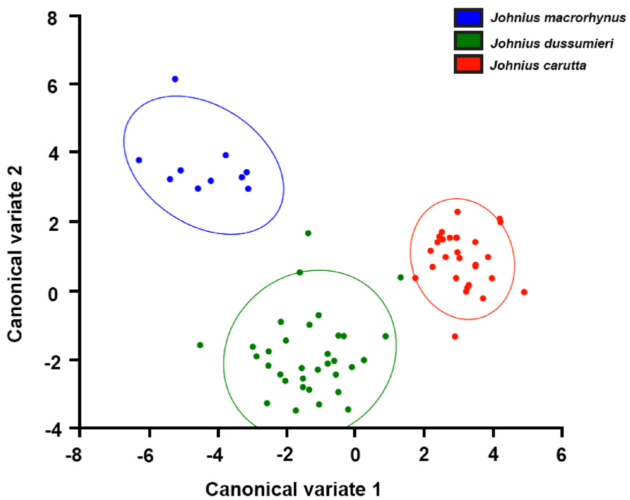

Fig. 4 Canonical variate analysis showing distinct clusters among the three sciaenid species

Table 2 DFA matrix of three species (family: Sciaenidae)

Name of the species	*J. carutta*	*J. dussumieri*	*J. macrorhynus*
J. dussumieri			
PD	0.08411238	–	–
MD	5.3298	–	–
T-sq. V	430.2928	–	–
P-value	< 0.0001	–	–
J. macrorhynus			
PD	0.10058857	0.08207196	–
MD	23.7794	6.4965	–
T-sq. V	4166.5637	323.8992	–
P-value	< 0.0001	< 0.0001	–

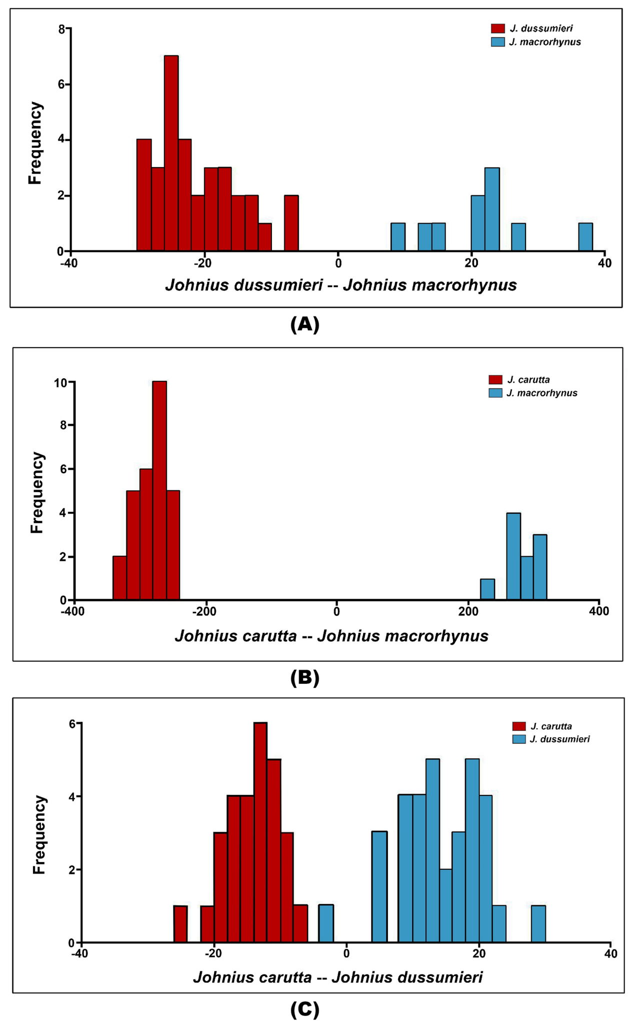

Fig. 5 The discriminant function analysis showing shape variation of otoliths between the three species. **A** *J. dussumieri and J. macrorhynus*; **B** *J. carutta and J. macrorhynus*; **C** *J. carutta* and *J. dussumieri*

macrorhynus. The species *J. dussumieri* has discriminant scores significantly different from *J. macrorhynus* and *J. carutta* ($p < 0.05$ at 95% significance level). Figure 5A–C) shows the discrimination of the shape of otolith between the three different species, *J. macrorhynus*, *J. dussumieri* and *J. carutta*.

Discussion

Most of studies focusing on GMA rely mostly on the morphology of fish bodies, with the goal of facilitating species classification and distinguishing morphological differences between juvenile and adult specimens (Ponton et al. 2013;

Tripathy et al. 2022; Santos et al. 2022; Kashani and Panhwar 2023). Comparative otolith morphology of sciaenids based on otolith length with body dimension was carried out by Kumar et al. (2012) along the Greater Mumbai coast. Farooq and Panhwar (2023) conducted an in-depth discriminant function analysis of nine commercially important sympatric catfish species of Pakistan, leveraging both otolith structure and morphological data to enhance species identification and understanding of their ecological dynamics. Limited studies have employed Geometric Morphometric Analysis (GMA) to explore otolith shape variation, notably in the works of Rogers (2015), Assis et al. (2020) and D'Iglio et al. (2021). These reports contribute valuable insights into the morphological differences among fish species, highlighting the potential of GMA as a tool for understanding ecological and evolutionary processes. However, there were no such previous studies on GMA based on otolith shape variation on the species of the genus *Johnius* along the east coast of India.

Therefore, the present study on GMA is the first of its kind for the mentioned species providing valuable insight into the shape variation concerning otoliths. The results from our Canonical Variate Analysis reveal a significant difference in the shape of otolith and the formation of distinct clusters among the three sciaenid species (Fig. 4), while the Discriminant Function Analysis further endorse these findings by effectively differentiating species (Fig. 5). The molecular phylogeny of the genus *Johnius*, which includes several commercially important species, has been explored in various studies. Research utilizing DNA sequencing techniques has revealed insights into the evolutionary relationships within this genus, highlighting distinct lineages and genetic diversity among species (Lakra et al. 2009; Lo et al. 2015; Li et al. 2018; Hanafi et al. 2023). Previous research has demonstrated that molecular data can enhance taxonomic resolution and offer valuable insights into speciation events within the *Johnius* taxon, particularly in relation to the ecological adaptations and biogeographic distribution of the species. GMA relies on morphological data to provide insights into phenotypic variation, species identification, and the effects of environmental factors on morphology in contrast molecular studies provide a genetic perspective on evolutionary relationships. Combining these approaches can lead to a more complete understanding ofthe diversity of a species.

This evidence highlights that landmark-based geometric morphometrics of otolith shape variation is a robust method for identifying sciaenid fish, reinforcing the notion that otoliths can provide critical insights into species differentiation. Moreover, extending geometric morphometric analysis to include other structures, such as dermal scales, may enhance our ability to distinguish among various fish groups. This expanded approach holds significant implications for fisheries management and biodiversity conservation, as accurate species identification is essential for implementing effective management strategies and protecting marine ecosystems.

However, while geometric morphometrics offers valuable insights, it is important to acknowledge its limitations. Relying solely on morphometric data may not provide a complete understanding of speciation and character divergence (see Seth et al. 2019). Therefore, we recommend integrating geometric morphometric studies with multiple molecular markers to achieve a more comprehensive view of evolutionary processes and adaptive mechanisms.

Conclusion

In conclusion, this study illustrates the promising role of otolith-based geometric morphometric analysis in enhancing taxonomic identification and informs future research directions that could further illuminate the complexities of fish diversity and evolutionary dynamics.

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Author contributions All authors contributed to the conception and design of the work. MP, NM and PS: sampling, data analysis, manuscript preparation; SKM and SR: conceptualization, data analysis, manuscript preparation and updating; JKS: conceptualization, critical analysis, manuscript preparation and updating. All authors read and approved the final manuscript.

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Declarations

Competing interests There is no conflict of interest among the authors for the publication.

Ethical approval The species under study are not listed in any protection categories of the Wild Life (Protection) Act, 1972 of India. Additionally, the otoliths were extracted from deceased fish collected with the assistance of local fishermen; therefore, ethical clearance certification is not applicable.

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