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Population-level morphological differentiation of *Gudusia chapra* (Hamilton, 1822) from three river systems of Bangladesh revealed by geometric morphometrics

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Abstract

Previous research has demonstrated that morphological variation among riverine populations often reflects local hydrological conditions, habitat structure, and restricted connectivity among drainage systems. Understanding population-level variation is critical for accurate taxonomic resolution and effective fisheries management of widely distributed freshwater species. This study examines morphological differentiation among three riverine populations of *Gudusia chapra* from the Atrai, Padma, and Brahmaputra rivers of Bangladesh using landmark-based geometric morphometrics. Ninety specimens were analyzed using 15 homologous landmarks, with non-shape variation removed by Generalized Procrustes Analysis (GPA), followed by population-level shape divergence evaluated using Principal Component Analysis (PCA), Relative Warp Analysis (RWA), Canonical Variate Analysis (CVA), and Discriminant Function Analysis (DFA). The first two principal components explained 98.23% of the total shape variance, with PC1 (94.64%) clearly separating the Brahmaputra specimens from those of Atrai and Padma. Pairwise RWA revealed strong morphological divergence between Atrai–Brahmaputra and Brahmaputra–Padma populations, with over 95% of the variance explained by the first two components. UPGMA cluster analysis grouped individuals into three well-defined clusters corresponding to the river systems, with the Brahmaputra population forming the most cohesive cluster and Atrai showing greater within-group dispersion. CVA and DFA further supported significant morphological structuring, with the Mahalanobis and Procrustes distances between populations statistically significant ($p < 0.01$) and an overall classification accuracy of 91.1%. These results demonstrated pronounced population-level shape divergence in *G. chapra*, likely driven by hydrological heterogeneity and localized environmental pressures. The study provides critical baseline information for stock-based management of this ecologically and commercially important species.

Keywords: *Gudusia chapra*; Geometric morphometrics; Population structure; Morphological divergence; Fisheries management

Introduction

Bangladesh is characterized by an extensive and intricate network of rivers, canals, floodplains, and wetlands that together form one of the richest freshwater ecosystems in the world. This hydrographic complexity sustains a high diversity of indigenous fish species, many of which play crucial roles in ecological functioning, food security, and rural livelihoods. Among the small indigenous species (SIS), *Gudusia chapra* (Hamilton, 1822), commonly referred to as river shad or chapila, is of considerable ecological, economic, and taxonomic interest. This small clupeid, belonging to the family Cyprinidae, is widely distributed throughout South Asia and occurs

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abundantly in the major river systems of Bangladesh, including the Padma, Jamuna, Brahmaputra, and Meghna (Rahman, 2005; Hossain et al., 2014). The hydrological and physicochemical characteristics of these river systems vary markedly, encompassing differences in flow regimes, substrate composition, turbidity, and other environmental parameters. Such environmental heterogeneity can promote intraspecific phenotypic divergence through local adaptation or phenotypic plasticity. In fishes, morphological traits such as body shape and fin configuration are closely linked to environmental variables, including water current, temperature, prey availability, and predation pressure (Räsänen & Hendry, 2008; Langerhans, 2010). For example, streamlined body forms are typically favored in lotic environments, whereas deeper body forms are more frequent in lentic habitats. The study of these morphological adaptations provides valuable insight into the population structure, evolutionary processes, and ecological interactions, all of which are fundamental to effective fisheries management and conservation. Traditional morphometric methods based on linear measurements have long been employed in fish taxonomy and stock identification. However, these approaches may overlook subtle but taxonomically significant shape variation. In recent decades, landmark-based geometric morphometric analysis (GMA) has emerged as a more powerful tool for quantifying shape, because it preserves the spatial relationships among anatomical landmarks while enabling multivariate statistical analysis (Rohlf & Marcus, 1993; Zelditch et al., 2012). Landmark-based geometric morphometric techniques, including Relative Warp Analysis (RWA), Principal Component Analysis (PCA), and Canonical Variate Analysis (CVA), are widely used to discriminate fish stocks and populations based on phenotypic variation. Recent studies have demonstrated their effectiveness in detecting environmentally driven shape divergence in *Channa striata* (Afzal Khan et al., 2019; Torres et al., 2020), identifying morpho-stocks of *Cirrhinus reba* across river systems (Ethin et al., 2019), and revealing population-level morphological structuring in clupeids such as *Tenualosa ilisha* (Dwivedi, 2019; Das et al., 2020). Although geometric morphometrics cannot resolve true cryptic species, for which molecular genetic approaches are essential, it provides a cost-effective framework for assessing phenotypic structuring and serves as a complementary tool to molecular methods in population differentiation and integrative taxonomy (Kelly et al., 2025; Cadrin et al., 2013). Techniques such as Relative Warp Analysis (RWA), Principal Component Analysis (PCA), and Canonical Variate Analysis (CVA) have been successfully applied to discriminate stocks and populations in a range of freshwater and marine fishes, including *Channa striata*, *Cirrhinus reba*, and *Tenualosa ilisha* (Afzal Khan et al., 2019; Cadrin et al., 2013). Such morphometric analyses are particularly valuable in cases where genetic differentiation is low or difficult to assess, as they can reveal cryptic structuring that may correspond to distinct evolutionary or management units. Traditional morphometric methods based on linear measurements have long been employed in fish taxonomy and stock identification; however, these approaches may overlook subtle but taxonomically informative shape variation. In contrast, landmark-based geometric morphometric analysis (GMA) has emerged as a powerful framework for quantifying shape because it preserves the spatial relationships among anatomical landmarks while allowing rigorous multivariate statistical analyses (Rohlf & Marcus, 1993; Zelditch et al., 2012). Landmark-based geometric morphometric techniques, including Relative Warp Analysis (RWA), Principal Component Analysis (PCA), and Canonical Variate Analysis (CVA), are widely applied to discriminate fish stocks and populations based on phenotypic variation. Their effectiveness has been demonstrated in detecting environmentally driven shape divergence in *Channa striata* (Afzal Khan et al., 2019; Torres et al., 2020), identifying morpho-stocks of *Cirrhinus reba* across river systems (Ethin et al., 2019), and revealing population-level morphological structuring in clupeids such as *Tenualosa ilisha* (Dwivedi, 2019; Das et al., 2020). Although geometric morphometrics alone cannot resolve true cryptic species, for which molecular genetic approaches are essential, it provides a cost-effective means of assessing phenotypic structuring and serves as a complementary tool to molecular methods in population differentiation and integrative taxonomy (Cadrin et al., 2013; Kelly et al., 2025). Despite the wide distribution and ecological importance of *G. chapra*, its population structure within Bangladesh remains poorly documented. Previous studies have largely focused on meristic counts, length–weight relationships, growth patterns, and condition factors (Ahmed et al., 2007; Azadi & Rahman, 2008; Das et al., 2020; Hossain et al., 2021). These studies indicate substantial spatial variability in growth and condition related to environmental factors such as temperature, dissolved oxygen, and pH (Jisr et al., 2018; Sultana et al., 2022). However, a systematic evaluation of the fine-scale morphological divergence using modern geometric morphometric tools has not yet been undertaken. Such information is essential for understanding population-level differentiation, which in turn has implications for taxonomy, stock identification, and the development of effective management and conservation strategies. Neglecting population-specific morphological variation risks overlooking distinct subpopulations that may represent important ecological or evolutionary units. The present study aims to address this gap by applying landmark-based geometric morphometric analysis to assess the morphological variation among *G. chapra* populations from three major river systems of Bangladesh. Specifically, the objectives are to: (i) quantify phenotypic variability among populations from different river basins; (ii) identify discrete morpho-stocks that may correspond to distinct management or evolutionary units; (iii) relate observed morphological patterns to ecological and hydrological factors; and (iv) establish baseline data for future monitoring of population structure under natural and anthropogenic influences. By integrating modern morphometric methods with an ecological context, this study contributes to a more comprehensive understanding of intraspecific variation in *G. chapra*, supporting both systematic research and evidence-based management of this ecologically significant clupeid.

Materials and Methods

Study period and research station

The study was conducted over a six-month period from July to December 2024. All morphometric measurements, imaging, and data processing were carried out in the Fisheries Biology and Genetics Laboratory of Hajee Mohammad Danesh Science and Technology University (HSTU), Dinajpur, Bangladesh.



Sampling sites

A total of 90 specimens of *Gudusia chapra* were collected from three river systems representing distinct hydrological regimes in Bangladesh, the Atrai (Naogaon), the Brahmaputra (Mymensingh), and the Padma (Rajshahi) where the species is known to occur (Rahman, 2005; Lama et al., 2014). Geographic coordinates were recorded at each site to ensure reproducibility. Although larger sample sizes can increase statistical power, the current sample size was constrained by the species' IUCN Red List status as Near Threatened (Chaudhry, 2010), necessitating ethical collection practices to minimize population impact. Despite this limitation, previous studies on freshwater cyprinids have demonstrated that morphometric analyses with 20–40 specimens per population are sufficient to detect population-level shape variation using geometric morphometrics (Farré et al., 2016; Rohlf, 2015). Therefore, the current sampling strategy represents a balance between methodological rigor and conservation responsibility. The number of specimens and corresponding site information are presented in Table 1, and the sampling locations are shown in Figure 1.

Table 1. Sampling sites and geographical coordinates of *Gudusia chapra* specimens.

Serial No.	Collection Site	Latitude–Longitude	n
01	Atrai River, Naogaon	24°36'50.1"N 88°58'08.3"E	30
02	Brahmaputra River, Mymensingh	24°43'34.0"N 90°26'33.2"E	30
03	Padma River, Rajshahi	24°21'46.0"N 88°35'23.1"E	30



Figure 1. Map showing the sampling sites of *Gudusia chapra*. Symbols indicate sampling sites, and connecting routes illustrate the relative spatial distribution of the study locations.

Sample collection and preservation

Specimens were collected between July and November using standard fishing gears, including cast nets, gill nets, and seine nets. Immediately after capture, the total length (TL) and body weight (BW) were measured using a digital caliper and an electronic balance, respectively. Thirty specimens per site were selected for morphometric analysis to ensure sufficient statistical power. The fish were

ethanized in accordance with institutional ethical guidelines. Standardized lateral photographs were taken immediately after measurement, and specimens were preserved in 10% buffered formalin for future reference and validation.

Digital image acquisition and standardization

Photographs were taken using a high-resolution DSLR camera (Canon EOS 700D) mounted on a fixed tripod to maintain a consistent focal distance. The specimens were positioned on their left lateral side on a flat background with a metric scale. The fins were gently extended using soft pins or plastic rulers to minimize deformation (Figure 2). All images were stored in high-resolution JPEG format and labelled with the specimen ID, date, site, and river system.

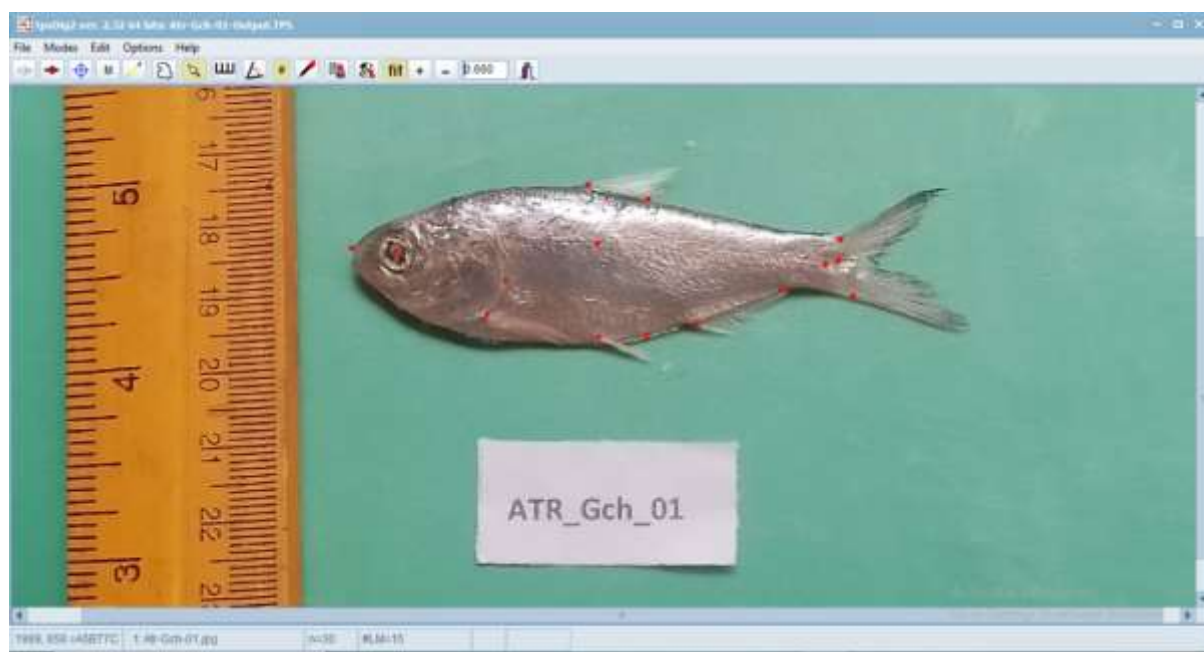


Figure 2. Standardized digital image acquisition of an Atrai River specimen (ATR_Gch_01)

Landmark selection and digitization

Fifteen homologous landmarks were selected following Zelditch et al. (2012) and previous studies on clupeid fishes (Table 2). These landmarks represent key anatomical points associated with swimming mechanics and hydrodynamics. Landmarks were digitized sequentially for all specimens and stored in TPS format for subsequent analyses.

Table 2. Landmark points used for the geometric morphometric analysis of *G. chapra*.

No.	Landmark Description	Anatomical Reference
1	Tip of snout	Rostral tip
2	Centre of eye	Eye centre
3	Posterior edge of operculum	Gill cover margin
4	Origin of dorsal fin	First dorsal fin ray base
5	End of dorsal fin	Last dorsal fin ray base
6	Origin of pectoral fin	First pectoral fin ray base
7	Origin of pelvic fin	First pelvic fin ray base
8	Origin of anal fin	First anal fin ray base
9	End of anal fin	Last anal fin ray base
10	Dorsal insertion of caudal fin	Caudal peduncle (upper)
11	Ventral insertion of caudal fin	Caudal peduncle (lower)
12	Centre of caudal fin (tip of hypural plate)	Midpoint of caudal base
13	Point above anus (between pelvic and anal fins)	Pre-anal midline
14	Mid-body along lateral line	Midway from snout to caudal base
15	End of lateral line or posterior belly edge (if absent)	Posterior margin of body

Data preprocessing and size standardization

To isolate shape variation independent of size, landmark configurations were aligned using Generalized Procrustes Analysis (GPA), which removes differences in position, orientation, and scale. Centroid size was calculated as a measure of overall body size. Procrustes coordinates were regressed against centroid size to account for allometric effects, and residuals were used as size-corrected shape variables for subsequent analyses. Data preprocessing was performed using the TPS series software and MorphoJ.

Multivariate shape analysis

Relative Warp Analysis (RWA) was employed to summarize major axes of shape variation among populations. Canonical Variate Analysis (CVA) was applied to visualize group separation, and Mahalanobis and Procrustes distances were calculated to quantify pairwise differences. Discriminant Function Analysis (DFA) with leave-one-out cross-validation was used to assess classification accuracy.

Statistical analyses

All morphometric analyses, including GPA, RWA, CVA, DFA, and distance metrics, were conducted using PAST v5.2.2. Significance was tested using MANOVA and permutation tests (1,000 iterations). ANOVA, regression, and correlation analyses between morphometric and size variables were performed using SPSS v25.0. Statistical significance was set at $p < 0.05$.

Results

Centroid size and shape analysis:

One-way ANOVA of centroid size showed no significant differences in overall body size among populations (ANOVA, $F = 2.71$, $df = 2, 87$, $p = 0.072$), indicating that size variation was not statistically significant. Because centroid size did not differ significantly among populations, a box plot for size comparison was not presented. In contrast, MANOVA based on shape variables revealed significant differences among populations ($p < 0.05$), demonstrating that morphological divergence is primarily driven by shape rather than size. Therefore, shape variation is illustrated using Relative Warp Analysis (RWA) scatter plots, which clearly depict population-level differentiation in body shape.

Principal component analysis (relative warp analysis)

Principal Component Analysis (PCA) of the Relative Warp scores revealed clear morphological separation among the *Gudusia chapra* populations from the Atrai, Padma, and Brahmaputra rivers (Table 3; Figure 3). The first two components accounted for 98.23% of the total shape variance, with PC1 explaining 94.64% and PC2 contributing 3.59%. Shape deformation patterns associated with PC1 indicated that the major axis of variation was primarily related to differences in overall body depth, head length, dorsal fin position, and caudal peduncle morphology, reflecting variation in body streamlining among river systems. The PCA scatter plot showed that specimens from the Brahmaputra River (\blacktriangle) formed a distinct cluster on the positive side of PC1, indicating pronounced morphological divergence from the other two populations. In contrast, the Atrai (\bullet) and Padma (\blacksquare) populations overlapped partially but remained separable along PC2, which was mainly associated with finer-scale variations in head shape, fin positioning, and posterior body profile suggesting moderate but detectable shape differentiation (Table 3; Figure 3A). This spatial arrangement reflects a structured inter-population variation, likely driven by environmental heterogeneity or restricted gene flow among river systems. Pairwise Relative Warp Analyses further supported these patterns. Between Atrai and Brahmaputra populations, strong shape differentiation was observed, with the first two components explaining 95.29% of the total variation and specimens forming distinct clusters along Component 1 (Table 3; Figure 3B), indicating divergence predominantly associated with body depth and caudal peduncle configuration, likely influenced by local hydrological conditions and habitat structure. Similarly, comparison between the Brahmaputra and Padma populations revealed clear morphological differentiation, with the first two components explaining 95.73% of the total variation (Table 3; Figure 3C). The two populations were distinctly separated along Component 1, further supporting pronounced shape divergence consistent with habitat-specific structuring across river systems.

Table 3. Eigenvalues and percentage of variation of the three *G. chapra* population based on Relative Warp Analysis.

Populations Sets	Eigen value		% Variance		
	PC-1	PC-2	PC-1	PC-2	Total % variance
Overall: three populations	790911	29969	94.642	3.586	98.228
Pairwise: Atrai-Brahmaputra	862769	26986	95.289	2.986	98.275
Pairwise: Brahmaputra-Padma	920450	26838	95.731	2.791	98.522



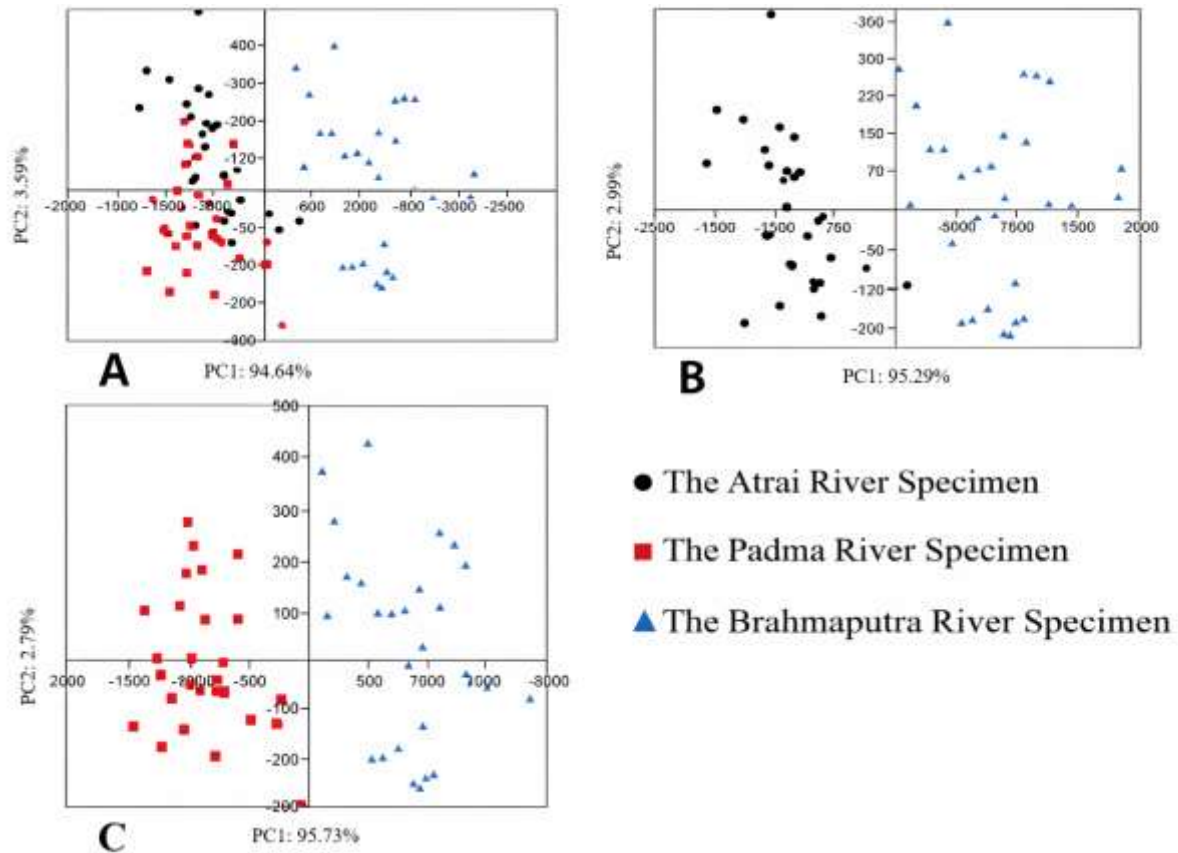


Figure 3. Pairwise Relative Warp Analysis (RWA) scatter plots showing morphological differentiation among *Gudusia chapra* populations from three river systems of Bangladesh. Black circles represent specimens from the Atrai River, red squares represent specimens from the Padma River, and blue triangles represent specimens from the Brahmaputra River. Panels show comparisons: (A) Atrai–Padma–Brahmaputra, (B) Atrai–Brahmaputra, and (C) Padma–Brahmaputra. The first two relative warps (RW1 and RW2) are plotted, with the percentage of shape variation explained by each axis indicated on the axes.

Cluster analysis (UPGMA)

The UPGMA dendrogram based on Procrustes distances derived from landmark-based geometric morphometric data revealed clear population-level structuring among *Gudusia chapra* specimens from the three river systems (Figure 4). Individuals from the Brahmaputra River formed a distinct and cohesive cluster, clearly separated from specimens collected from the Atrai and Padma rivers. In contrast, Atrai and Padma specimens showed closer affinity, with partial intermixing within a broader cluster, although several subclusters corresponding to each river were still evident. The clustering pattern indicates marked morphological differentiation of the Brahmaputra population, while comparatively greater within-group dispersion was observed among Atrai and Padma populations.

Table 5. Cross-validated classification matrix (% correct classification)

Actual Group	Classified as Atrai	Classified as Padma	Classified as Brahmaputra	Correct (%)
Atrai	21	2	1	87.5
Padma	3	15	1	88.2
Brahmaputra	1	0	29	96.7

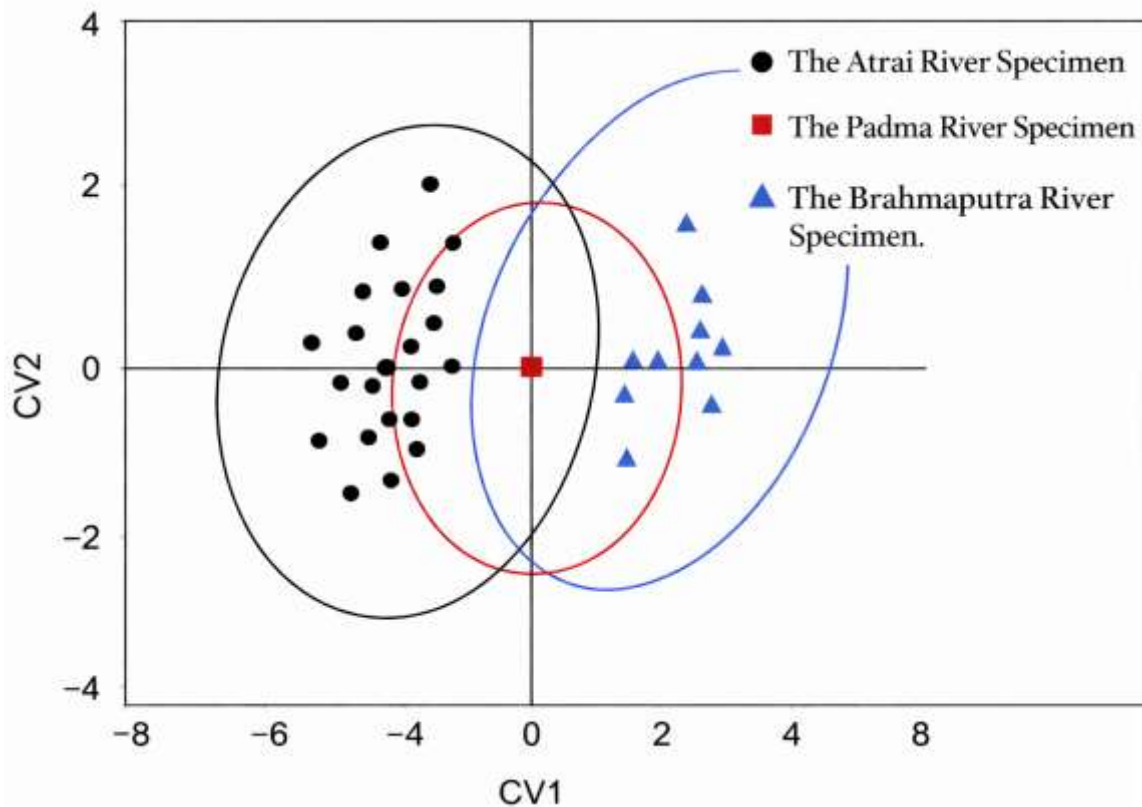


Figure 5. Canonical variate analysis (CVA) scatter plot showing shape variation among *Gudusia chapra* populations from three rivers. Black circles represent specimens from the Atrai River, red squares represent specimens from the Padma River, and blue triangles represent specimens from the Brahmaputra River. The first two canonical variates (CV1 and CV2) are plotted, and the ellipses indicate the 95% confidence regions for each population, illustrating the degree of overlap and separation in body shape among river populations.

Across all analyses (PCA, RWA, cluster analysis, CVA, and DFA), the Brahmaputra population exhibited the most distinct body shape, whereas the Padma and Atrai populations displayed moderate but significant differentiation. The combination of multivariate approaches confirmed strong inter-population shape divergence in *G. chapra*, consistent with the influence of hydrological variation and habitat-specific selective pressures. These findings highlight the utility of geometric morphometrics for delineating the population structure in riverine fishes.

Discussion

The geometric morphometric analyses revealed clear and statistically significant morphological differentiation among the *Gudusia chapra* populations from the Atrai, Padma, and Brahmaputra rivers. The separation observed in PCA, RWA, CVA, and DFA strongly indicates population-level structuring, with the Brahmaputra population emerging as the most distinct morphologically. This pattern suggests that environmental heterogeneity and hydrological variation among river basins play a central role in shaping phenotypic divergence within this species. Morphological variation in fishes often reflects adaptive responses to local environmental conditions, including flow regime, substrate type, prey availability, and predator pressure (Räsänen & Hendry, 2008; Langerhans, 2010). Riverine systems in Bangladesh differ considerably in their hydrology and physicochemical characteristics (Rahman, 2005; Hossain et al., 2014). The Brahmaputra River, for example, is characterized

by higher flow velocity, seasonal flooding, and dynamic channel morphology compared to the more regulated flow of the Padma or Atrai systems. Such conditions likely impose distinct selective pressures that favor streamlined body shapes in fast-flowing habitats to enhance swimming efficiency and energy conservation (Imre et al., 2002; Keeley et al., 2007). The pronounced morphological separation of the Brahmaputra population along PC1 is consistent with this ecological context. The moderate but significant differentiation observed between the Atrai and Padma populations may reflect subtle hydrological and ecological differences between these systems. Partial overlap in morphospace indicates some degree of shared environmental influences or possible gene flow between adjacent river systems. Similar patterns of population-level morphological structuring driven by local environmental gradients have been documented in other South Asian riverine fishes, including *Channa striata* (Afzal Khan et al., 2019), *Cirrhinus reba* (Ethin et al., 2019), and *Tenualosa ilisha* (Vaisakh et al., 2020). These studies, like the present one, demonstrate that geometric morphometrics can effectively detect fine-scale population divergence even in species with limited genetic differentiation. Cluster analysis further supported the existence of three distinct morphometric groups corresponding to the sampled rivers, while CVA and DFA confirmed high classification accuracy (91.1%), underscoring the reliability of landmark-based morphometric approaches for population discrimination. Similar levels of classification success have been reported in morphometric studies of cyprinids and clupeids, where shape variation has been linked to ecological segregation, migration barriers, and hydrographic differences (Cadrin, 2000; Bookstein, 1991; Rohlf & Marcus, 1993; Zelditch et al., 2012). From a taxonomic and biosystematics perspective, the observed morphological divergence among *Gudusia chapra* populations likely reflect population structuring below the species level, with implications for identifying Evolutionarily Significant Units (ESUs) or Management Units (MUs) (Fraser & Bernatchez, 2001; Hoelzel, 2023; Robertson et al., 2014; Casacci et al., 2014). The greatest shape changes among the three populations were associated primarily with overall body depth, head length, dorsal fin position, and caudal peduncle morphology, which collectively represent functionally important traits related to swimming performance and habitat use. These characters exhibited pronounced differentiation in the Brahmaputra population, characterized by a more streamlined body profile and a relatively narrower caudal peduncle, consistent with adaptation to high-flow, turbid, and hydrodynamically complex environments. Morphological variation in fish body shape is often correlated with environmental conditions such as flow regime, where individuals from high-velocity habitats tend to exhibit more streamlined bodies and narrower caudal peduncles that reduce drag and enhance swimming efficiency, whereas fish from slower or structurally complex environments display deeper bodies that improve maneuverability and stability (Langerhans et al., 2003; Langerhans, 2008; Leavy et al., 2009; Kelley et al., 2017). In contrast, individuals from the Atrai and Padma rivers tended to display comparatively deeper bodies and subtle shifts in fin positioning and head shape, features commonly associated with lower flow regimes, heterogeneous substrates, and greater habitat complexity (Webb, 1984; Winemiller, 1991; Langerhans, 2008; Webster et al., 2011). Although this study focused on phenotypic traits, such morphological differentiation often parallels genetic structuring, especially in geographically isolated or environmentally distinct populations. Geometric morphometrics provides a powerful first step in delineating population boundaries, particularly in regions such as Bangladesh, where molecular data remain limited for many indigenous species. The findings also have practical implications for fisheries management and conservation. *G. chapra* is a commercially important small indigenous species whose populations are subject to intense fishing pressure and habitat alteration. Recognizing population-specific morphological variation can inform stock-based management strategies, including targeted conservation measures, habitat protection, and restocking programs (Cadrin et al., 2013). Failure to account for population structure can lead to inappropriate management decisions that overlook distinct stocks, thereby compromising long-term population viability. Finally, the study highlights the value of geometric morphometrics as a low-cost, robust, and sensitive approach for detecting population structure in data-deficient contexts. Integrating morphometric data with genetic, ecological, and otolith microchemistry analyses in future work would provide a more comprehensive understanding of the population connectivity and evolutionary processes in *G. chapra*. Such integrative approaches are increasingly important for effective biodiversity assessment and the delineation of taxonomic and management units in riverine fish species (Campbell et al., 2015; Quadroni et al., 2023).

Conclusion

This study provides clear evidence of the population-level morphological divergence in *Gudusia chapra* across three major river systems of Bangladesh. Landmark-based geometric morphometric analyses consistently revealed distinct shape patterns, with the Brahmaputra population emerging as the most differentiated and the Atrai and the Padma populations displaying moderate but significant divergence. These findings underscore the utility of geometric morphometrics as a robust, cost-effective tool for detecting fine-scale population structure in freshwater fishes. From a taxonomic perspective, the observed morphological structuring may indicate underlying evolutionary differentiation, meriting further integrative research using molecular and ecological data. From a management standpoint, recognizing population-specific variation is critical for the development of stock-based conservation and fishery management strategies. By bridging morphometric evidence with ecological and taxonomic insights, this study establishes a baseline for identifying distinct management units within *G. chapra*, supporting both the conservation of its intraspecific diversity and the sustainable exploitation of this ecologically and economically important species.



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