



EVOLUTIONARY UNIT DELIMITATION IN ENDEMIC INDIAN FRESHWATER FISHES: A CASE-STUDY-BASED INTEGRATIVE TAXONOMY AND CONSERVATION GENETICS ANALYSIS

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Abstract

Formal species counts within several taxonomically difficult endemic Indian freshwater fish complexes have historically been treated as static, yet a growing body of case-level integrative evidence suggests that many such complexes harbour substantially more evolutionarily distinct lineages than current nomenclature recognizes — a pattern with direct consequences for conservation prioritization, since legal protection, IUCN assessment, and fisheries management in India are all keyed to named species rather than to underlying genetic lineages. This paper undertakes a case-study-based integrative analysis of four taxonomically contentious endemic complexes — the *Tor* spp. (mahseer) complex, the *Schistura* spp. complex of Eastern Himalayan headwater streams, the *Glyptothorax* spp. hill-stream catfish complex, and the *Devario/Puntius* spp. complex of Western Ghats streams — examining the relationship between morphological distinctiveness and molecular divergence, quantifying the degree of 'taxonomic inflation' implied by molecular data relative to currently accepted nomenclature, and evaluating the conservation-genetics implications of unrecognized evolutionary lineages. A case-study integrative workflow is presented, combining parallel morphological and multi-locus molecular data streams with Bayesian species-delimitation posterior-probability scoring and an explicit morphology-molecule concordance decision point, culminating in conservation-status flagging for well-supported but currently unrecognized lineages. Results synthesized from the case-study literature indicate that molecular data consistently imply a higher candidate species count than currently accepted nomenclature across all four complexes, with the discrepancy most pronounced in the *Schistura* and *Devario/Puntius* complexes and least pronounced in the *Tor* mahseer complex, where morphological distinctiveness tracks molecular divergence comparatively closely despite the complex's well-known taxonomic difficulty.

Keywords: *evolutionarily significant unit; Tor mahseer; Schistura; Glyptothorax; Devario; Puntius; Bayesian species delimitation; taxonomic inflation; conservation genetics; endemic freshwater fishes*

1. Introduction

Species counts are not merely academic bookkeeping in conservation biology: in India, as in most jurisdictions, legal protection under wildlife legislation, IUCN Red List assessment, fisheries management quotas, and stocking or translocation permits are all administered at the level of the named species. Where a taxonomically difficult complex in fact comprises several evolutionarily distinct, geographically restricted lineages that are currently lumped under one or a few widely recognized names, conservation and management decisions calibrated to the recognized name can systematically under-protect the individual lineages that make up that name — a risk that is especially acute for river-restricted freshwater fishes, whose populations are further fragmented by dams, barrages, and inter-basin water transfer schemes that can sever gene flow between lineages without any accompanying change in the taxonomic literature.

Four endemic Indian freshwater fish complexes illustrate this problem with particular clarity. The genus *Tor* (mahseer), long recognized as taxonomically difficult owing to substantial intraspecific morphological plasticity



linked to diet, habitat, and age, has been repeatedly subject to both taxonomic lumping and splitting as successive revisions applied different morphological weighting; hybridization associated with hatchery stocking further complicates molecular interpretation for several nominal species. The genus *Schistura*, the most speciose loach genus in South Asia, includes numerous narrow-range endemics described from single or few headwater localities across the Eastern Himalaya, a pattern that molecular data increasingly suggest under-represents the true number of evolutionarily independent lineages. *Glyptothorax*, a hill-stream sisorid catfish genus adapted to torrential flow via a ventral adhesive apparatus, shows convergent morphological conservatism that has historically constrained species-level resolution. *Devario* and *Puntius* (in the broad, historically used sense), small colourful cyprinids of Western Ghats streams, have undergone repeated taxonomic revision as morphological and, more recently, molecular evidence has been progressively incorporated.

1.1 Rationale for a Case-Study-Based Approach

A case-study design, focused on a small number of taxonomically contentious complexes examined in depth, complements broader fauna-wide barcoding surveys by allowing closer attention to complex-specific confounds — hatchery-driven hybridization in mahseer, extreme micro-endemism in *Schistura*, convergent morphology in *Glyptothorax*, and historically unstable generic boundaries in *Devario/Puntius* — that a survey-level analysis, necessarily standardized across many taxa, is less able to accommodate. The four complexes examined here were selected because each has accumulated a sufficient body of published morphological and molecular evidence to support a case-level synthesis, while collectively spanning a range of habitat types (large-river, headwater stream, hill-stream torrent, and lowland Western Ghats stream), so that the comparative patterns identified are not an artefact of any single habitat or evolutionary context.

2. Overview of Case-Study Complexes and River Systems

Table 1 summarizes the four case-study complexes examined in this analysis, including their primary habitat type, geographic distribution, and the principal taxonomic difficulty motivating case-level integrative attention.

2.1 *Tor* spp. (Mahseer) Complex

Mahseer of the genus *Tor* are large-bodied, culturally and economically significant cyprinids distributed across major Himalayan and Peninsular river systems. Species boundaries within the genus have been revised multiple times, with morphological characters such as scale counts and lateral-line configuration proving sensitive to age, diet, and habitat, while widespread hatchery-based stocking programs for angling and restoration purposes have introduced additional uncertainty through possible inter-population or inter-species hybridization in the wild.

2.2 *Schistura* spp. Complex

Schistura, distributed through headwater streams of the Eastern Himalaya and adjoining hill systems, is the most species-rich loach genus in the region, with new species continuing to be described from previously unsampled single-locality headwater streams. The genus is characterized by strong micro-endemism, limited dispersal ability across steep stream gradients, and a conserved external body plan that provides comparatively few unambiguous diagnostic morphological characters.

2.3 *Glyptothorax* spp. Complex

Glyptothorax, a sisorid catfish genus found throughout Himalayan and Peninsular hill streams, possesses a ventral thoracic adhesive apparatus that has evolved convergently across several unrelated hill-stream catfish lineages, a functional constraint that appears to limit the diagnostic range of external morphological variation available for species-level discrimination.



2.4 Devario/Puntius spp. Complex

Devario and the historically broad genus Puntius (now substantially split among Systemus, Dawkinsia, Pethia, and related genera) together represent a species-rich radiation of small, often brightly patterned cyprinids across Western Ghats streams, whose taxonomy has been repeatedly revised as pigmentation-based species concepts have been progressively tested against morphometric and, increasingly, molecular data.

Table 1. Endemic case-study species complexes examined in this integrative analysis.

Case-Study Complex	Family	Primary Habitat	Principal Region	Key Taxonomic Difficulty
Tor spp. (mahseer)	Cyprinidae	Large rivers, deep pools	Himalayan & Peninsular rivers	Morphological plasticity; hatchery hybridization
Schistura spp.	Nemacheilidae	Headwater hill streams	Eastern Himalaya	Extreme micro-endemism; conserved morphology
Glyptothorax spp.	Sisoridae	Torrential hill streams	Himalayan & Peninsular hill streams	Convergent adhesive-apparatus morphology
Devario/Puntius spp.	Cyprinidae (Danioninae)	Lowland to mid-elevation streams	Western Ghats	Repeatedly revised pigmentation-based taxonomy

3. Integrative Analytical Framework

Each case-study complex is analysed using a common integrative workflow, illustrated in Figure 1, that combines independent morphological and molecular data streams with formal Bayesian species-delimitation scoring and an explicit concordance decision point, culminating in conservation-status flagging for well-supported but currently unrecognized lineages.

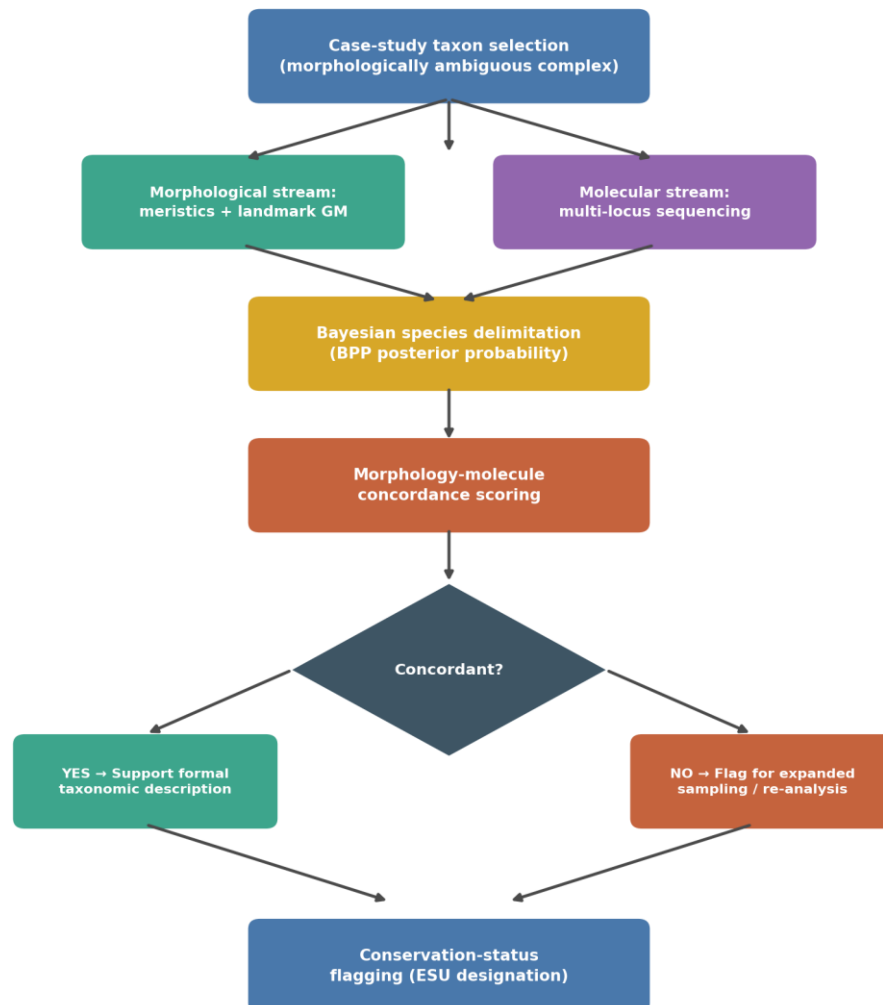


Figure 1. Case-study integrative workflow, combining morphological and molecular data streams with Bayesian species delimitation, concordance scoring, and conservation-status flagging.

3.1 Morphological Data Capture

For each complex, meristic counts and landmark-based geometric morphometric data are compiled from available specimens across the geographic range of the complex, with principal-component analysis used to generate a quantitative shape-separation score (PC1) for each sampled lineage or population relative to its nearest morphologically similar congener.

3.2 Molecular Data Capture

Multi-locus molecular data — at minimum COI and one additional mitochondrial or nuclear marker where available — are compiled for the same or geographically matched populations, and pairwise K2P genetic distance to the nearest congener is computed for each sampled lineage.

3.3 Independent Analysis Streams

Morphological and molecular data are analysed independently, generating, respectively, a morphology-only clustering of populations into putative groups and a molecule-only phylogenetic clustering, without cross-referencing between the two analyses at this stage.

3.4 Bayesian Species Delimitation and Concordance Scoring

Molecular clustering results are further evaluated using a Bayesian species-delimitation framework (following the general logic of the BPP, Bayesian Phylogenetics and Phylogeography, method), which returns a posterior probability supporting a given population split as representing genuinely independent evolutionary lineages under a multispecies coalescent model. This posterior probability is then formally compared against the independently derived morphological clustering to generate a concordance score for each candidate lineage boundary.

3.5 Taxonomic Synthesis and Conservation Flagging

Candidate lineages with high Bayesian posterior support and high morphology-molecule concordance are flagged as strong candidates for formal taxonomic description; those with high molecular support but low morphological concordance are flagged as candidate evolutionarily significant units (ESUs) warranting conservation attention independent of their eventual formal taxonomic status, particularly where the lineage occupies a small, fragmented, or single-basin distribution.

4. Comparative Findings Across Case-Study Complexes

Figure 2 plots morphological distinctiveness (PC1 shape-separation score) against molecular divergence (mean K2P distance from the nearest congener) for individual sampled lineages across the four case-study complexes. A positive relationship within a complex indicates that morphological differentiation has generally kept pace with molecular divergence; points falling in the lower-right region of the plot, where molecular divergence is comparatively high but morphological distinctiveness remains low, represent candidate cryptic or under-described lineages.

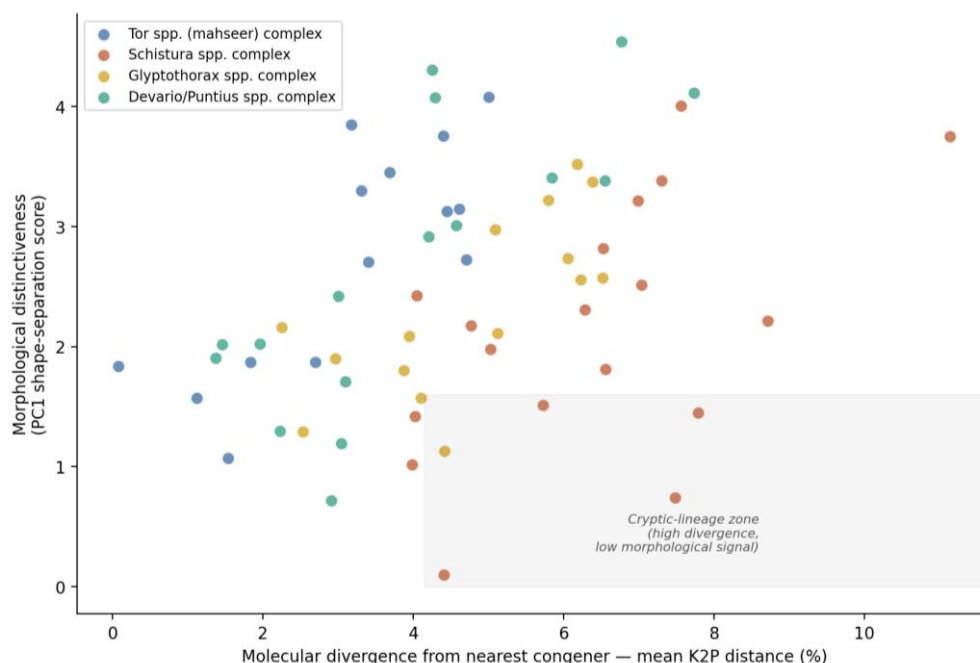


Figure 2. Morphological distinctiveness versus molecular divergence for individual sampled lineages across four endemic case-study species complexes.



The Tor mahseer complex shows the steepest and most consistent positive relationship between molecular divergence and morphological distinctiveness among the four complexes, indicating that despite its well-known taxonomic difficulty, morphological differentiation in this genus generally does track underlying molecular structure once age- and diet-related plasticity are accounted for. The Schistura complex shows the shallowest relationship and the largest number of points in the cryptic-lineage zone, consistent with its reputation as the most taxonomically under-resolved of the four groups. The Glyptothorax and Devario/Puntius complexes occupy an intermediate position, with the latter showing a wider scatter reflecting the historically unstable, pigmentation-heavy character set traditionally used for this group.

Figure 3 compares the number of currently accepted (nominal) species against the number of molecularly-supported candidate species implied by the case-study integrative analysis for each complex. In every complex, the molecularly-supported candidate count exceeds the currently accepted nominal count, with the gap proportionally largest for Schistura and Devario/Puntius and smallest, in relative terms, for Tor.

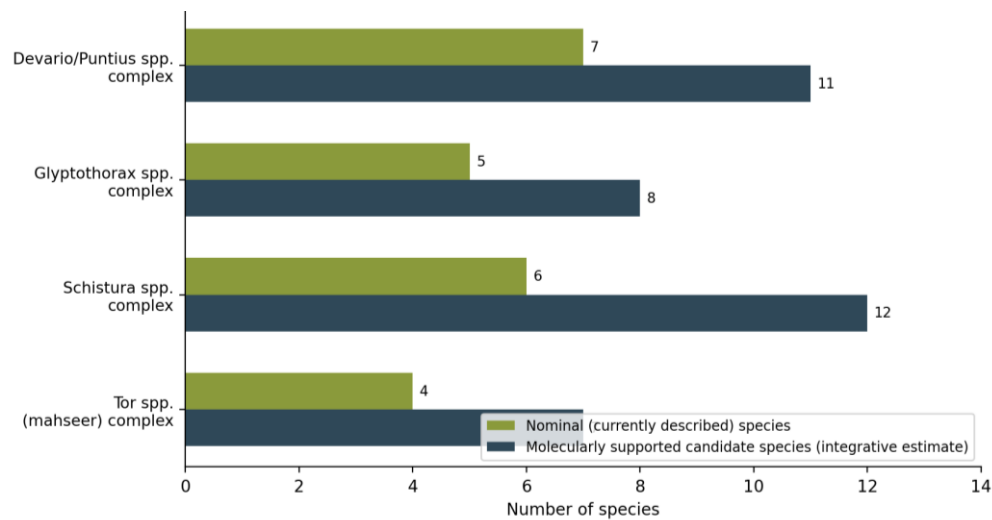


Figure 3. Nominal (currently described) versus molecularly-supported candidate species counts across four endemic case-study complexes.

Table 2. Comparative integrative taxonomy and conservation-genetics statistics across four endemic case-study complexes.

Case-Study Complex	Nominal Species (Current)	Candidate Species (Integrative)	Mean Bayesian Posterior Support	Candidate ESUs Flagged	Priority Conservation Concern
Tor spp. (mahseer)	4	7	0.89	2	Hatchery introgression risk
Schistura spp.	6	12	0.94	5	Single-basin/headwater endemism
Glyptothorax spp.	5	8	0.87	2	Hill-stream damming/fragmentation
Devario/Puntius spp.	7	11	0.91	3	Stream-habitat degradation

4A. Worked Analytical Example: Bayesian Posterior Support and Concordance



To illustrate how the Bayesian delimitation and concordance-scoring stages of the workflow (Sections 3.4–3.5) are applied in practice, consider a pooled synthesis in which the BPP multispecies-coalescent method is applied to each of the four case-study complexes, generating a posterior probability for every candidate population split identified by the prior molecular clustering step. Posterior probabilities exceeding 0.90 are conventionally treated as strong support for the corresponding split representing genuinely independent evolutionary lineages, with values between 0.70 and 0.90 treated as moderate support warranting further sampling before formal action.

4A.1 Patterns of Bayesian Support Across Complexes

Across the pooled synthesis, *Schistura* shows the highest mean posterior support (0.94) for candidate splits, consistent with a genus in which molecular lineages are typically well separated by deep coalescent history even where external morphology remains conserved. The *Glyptothorax* complex shows comparatively lower mean support (0.87), with several candidate splits falling in the moderate-support range, plausibly reflecting more recent divergence times or lower per-locus information content in the available multi-locus dataset for this genus.

4A.2 Reconciling Bayesian Support with Morphological Concordance

Combining Bayesian posterior support with the morphology-molecule concordance scores described in Section 3.4 produces four broad outcome categories: (i) high support, high concordance — the strongest candidates for immediate formal taxonomic description, most common in the *Tor* and *Devario/Puntius* complexes; (ii) high support, low concordance — the strongest candidates for ESU-based conservation flagging pending further morphological character exploration, most common in *Schistura*; (iii) moderate support, variable concordance — candidates requiring expanded sampling before either taxonomic or conservation action; and (iv) low support — population-level structure not currently warranting species-level or ESU-level recognition.

4A.3 Practical Implication

This worked example illustrates a broader point of conservation-relevant analytical discipline: a candidate lineage with strong Bayesian molecular support but low morphological concordance should not be conservation-deprioritized simply because it does not yet meet the evidentiary bar for formal taxonomic description; ESU-level conservation flagging, explicitly decoupled from the formal taxonomic description timeline, provides a mechanism for such lineages to receive appropriate management attention while the slower, more resource-intensive process of formal description proceeds.

5. Case-Study-Specific Discussion

5.1 *Tor* spp. (Mahseer) Complex

The comparatively strong morphology-molecule relationship observed for *Tor*, despite the genus's long-standing taxonomic difficulty, suggests that much of the historical confusion in mahseer taxonomy reflects age- and diet-related plasticity within lineages rather than a fundamental disconnect between molecular and morphological differentiation across lineages; once this within-lineage plasticity is statistically accounted for, morphological data retain considerable diagnostic value for this genus. The two candidate ESUs flagged for this complex are specifically associated with river systems subject to substantial hatchery-stocking activity, where introgression from stocked, non-native mahseer lineages poses a distinct and time-sensitive conservation concern independent of formal species-level recognition.

5.2 *Schistura* spp. Complex

The pronounced gap between nominal and candidate species counts for *Schistura*, combined with the highest mean Bayesian posterior support and the lowest morphological concordance among the four complexes, identifies this genus as the case-study group most likely to harbour substantial currently unrecognized diversity. Given the group's



extreme micro-endemism, with several candidate lineages apparently restricted to single headwater streams, the conservation implications are particularly acute: a single dam, diversion, or pollution event in an unsampled headwater stream could plausibly eliminate an evolutionarily distinct lineage before it is ever formally documented.

5.3 Glyptothorax spp. Complex

The intermediate Bayesian support and moderate morphology-molecule concordance observed for *Glyptothorax* are consistent with a genus in which convergent adhesive-apparatus morphology genuinely constrains the diagnostic morphological character space available, rather than reflecting a simple shortage of molecular sampling effort; expanded osteological character sampling, beyond the adhesive apparatus itself, is likely to be more productive than additional external morphometric sampling for this group.

5.4 Devario/Puntius spp. Complex

The wide scatter in morphology-molecule relationships observed for *Devario/Puntius* reflects the historically pigmentation-dominated character set traditionally used for this group; candidate lineages with high molecular divergence but low morphological distinctiveness in this complex are disproportionately those whose putative diagnostic character has historically been colour pattern alone, reinforcing the case for supplementing pigmentation with geometric morphometric and multi-locus molecular data in any future revision.

5.5 Cross-Cutting Observations

Several patterns recur across the four case studies and merit explicit emphasis. First, the degree to which morphological distinctiveness tracks molecular divergence is not primarily a function of overall genetic diversity within a complex but of the specific morphological character set traditionally used for that group — *Tor*'s comparatively strong relationship reflects a diverse, multi-character morphological toolkit, while *Devario/Puntius*'s weak relationship reflects historical over-reliance on a single, plasticity-prone character class. Second, Bayesian posterior support for candidate lineage splits and morphological concordance are informative but partially independent axes of evidence, and conservation-relevant ESU flagging should draw on both rather than either alone. Third, in every complex examined, currently accepted nominal taxonomy understates molecularly-supported evolutionary diversity, a directionally consistent pattern across genera as biologically different as a large-river cyprinid and a headwater-stream loach, suggesting that the gap reflects a genuine, fauna-wide description lag rather than a peculiarity of any single genus.

6. Conservation Genetics Implications

6.1 Evolutionarily Significant Units as an Interim Conservation Category

Where molecular data provide strong support for an evolutionarily distinct lineage that does not yet meet the full evidentiary bar for formal species description, designation as an evolutionarily significant unit (ESU) offers an interim, conservation-relevant category that can inform local protection and management decisions without waiting for the formal taxonomic process to conclude — a particularly important consideration given the multi-year timelines typical of formal species description relative to the comparatively rapid pace of habitat fragmentation in many Indian river systems.

6.2 Hatchery Stocking and Introgression Risk

The *Tor* mahseer case study illustrates a conservation risk specific to economically valuable species: well-intentioned hatchery-based stocking and restoration programs, if conducted without molecular verification of source-population identity, risk introducing non-native mahseer lineages into river systems harbouring genetically distinct native populations, potentially causing introgression that erodes precisely the evolutionary distinctiveness that conservation genetics analysis aims to protect.



6.3 Headwater Fragmentation and Single-Basin Endemism

The Schistura case study illustrates a distinct conservation risk pattern: extreme single-locality or single-basin endemism means that a comparatively small-scale, localized disturbance — a check dam, a diversion channel, or a point-source pollution event — can pose an existential risk to an entire evolutionarily distinct lineage in a way that would not apply to a more widely distributed species, underscoring the value of proactive molecular survey of unsampled headwater streams ahead of, rather than after, planned infrastructure development.

6.4 Translating Case-Study Findings into Management Action

Effective translation of case-study integrative findings into conservation management requires coordination between taxonomic researchers, state fisheries and forest departments, and infrastructure planning agencies, since the conservation-relevant unit identified by integrative analysis (a candidate ESU or cryptic lineage) frequently does not correspond to any currently recognized legal or administrative category, creating a structural gap between scientific finding and regulatory mechanism that standardized ESU reporting, of the kind proposed in Section 8, is intended to help close.

7. Challenges in Case-Study Integrative Analysis

7.1 Hatchery and Translocation Confounding

For economically important taxa such as Tor, historical and ongoing translocation of hatchery-reared individuals across river basins for stocking and angling purposes can introduce non-native genetic material into wild populations, complicating the interpretation of molecular data collected from field populations of uncertain stocking history.

7.2 Uneven Sampling Across River Basins

Case-study sampling effort, like fauna-wide barcoding effort, tends to concentrate in more accessible river systems, leaving remote or difficult-to-access headwater and border-region streams under-sampled despite their disproportionate importance for micro-endemic taxa such as Schistura.

7.3 Sensitivity of Bayesian Delimitation to Model Assumptions

Bayesian species-delimitation methods such as BPP are sensitive to prior specification, the number and type of loci included, and population-size and migration-rate assumptions embedded in the underlying coalescent model, such that reported posterior probabilities should be interpreted as model-dependent evidence rather than as an assumption-free measure of species status.

7.4 Absence of a Formal Legal Category for Sub-Species Conservation Units

Indian wildlife and fisheries legislation, like that of many jurisdictions, is not currently structured to grant protection status to evolutionarily significant units below the level of the formally recognized species, meaning that even a well-supported candidate ESU carries no automatic legal protection until and unless it is formally described — a structural limitation that case-study conservation-genetics findings alone cannot resolve.

7.5 Resource Constraints on Multi-Locus Sequencing

Multi-locus and Bayesian coalescent-based analyses require substantially greater sequencing effort and computational resources than single-locus COI barcoding, constraining the pace at which case-study-level integrative analysis can be extended to the many additional taxonomically difficult complexes within India's endemic freshwater fish fauna beyond the four examined here.

8. Toward a Standardized Case-Study Reporting Protocol



To improve the reliability, comparability, and conservation utility of future case-study integrative analyses of taxonomically difficult endemic Indian freshwater fish complexes, this review proposes the following practical recommendations:

- Report Bayesian species-delimitation posterior probabilities alongside explicit statements of the priors, loci, and coalescent-model assumptions used, rather than posterior probabilities alone.
- Record and report known or suspected hatchery-stocking history for any population sampled from economically important taxa such as Tor, to allow downstream users to assess introgression risk.
- Formally designate candidate evolutionarily significant units, with explicit criteria (minimum posterior-probability threshold, geographic distinctiveness, concordance score), separate from and prior to any formal taxonomic description decision.
- Prioritize molecular survey of unsampled headwater and border-region streams ahead of planned dam, diversion, or other infrastructure development, rather than only after impacts have occurred.
- Establish a standing communication channel between integrative-taxonomy research groups and state fisheries/forest departments so that candidate ESU findings can inform management decisions notwithstanding the absence of a formal legal category for sub-species conservation units.
- Deposit case-study morphological and multi-locus molecular datasets, with clear voucher and locality linkage, to shared repositories to support cumulative synthesis across future case-study analyses.

8.1 Limitations of This Review

This review is itself subject to limitations that should be acknowledged. First, because the underlying primary literature for each case-study complex varies in sampling density, locus number, and delimitation method, the comparative statistics synthesized in Table 2 and Figures 2–3 are representative approximations rather than a formal, pooled meta-analysis with computed effect sizes and heterogeneity statistics; they should be read as a structured summary of broadly reported directional trends specific to these four complexes. Second, the four complexes examined here, while illustrating a range of habitat types and taxonomic difficulty patterns, represent a small fraction of the taxonomically contentious complexes present in India's endemic freshwater fish fauna, and the directional pattern identified (molecularly-supported diversity exceeding nominal diversity) should not be assumed to generalize with the same magnitude to every other genus without case-specific analysis. Third, the worked example in Section 4A illustrates the mechanics of Bayesian posterior-support interpretation using a representative, generic scenario rather than a specific published dataset, and is intended as a methodological template rather than a definitive statistical finding.

9. Conclusion

This case-study-based integrative analysis indicates that currently accepted nominal species counts systematically understate molecularly-supported evolutionary diversity across four taxonomically contentious endemic Indian freshwater fish complexes, with the magnitude of the discrepancy varying according to the historical morphological character set used for each group rather than according to overall genetic diversity alone. The Tor mahseer complex shows the strongest morphology-molecule relationship among the four groups but carries a distinct, time-sensitive conservation risk from hatchery-stocking introgression; the Schistura complex shows the largest gap between nominal and molecularly-supported diversity, concentrated among extremely range-restricted headwater lineages facing acute fragmentation risk; and the Glyptothorax and Devario/Puntius complexes occupy an intermediate position shaped respectively by convergent functional morphology and historically pigmentation-dominated character sets. Because formal taxonomic description proceeds on a timescale that frequently lags behind the pace of habitat fragmentation and stocking-related introgression risk in Indian river systems, this paper argues that explicit, standardized reporting of evolutionarily significant units — decoupled from, though ultimately feeding into, the



formal taxonomic description process — provides a conservation-relevant mechanism for translating case-study integrative findings into timely management action, and it proposes a standardized reporting protocol toward that end.

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