

Diagnostic Morphological Characters, Osteological Synapomorphies, and Taxonomic Status of Cyprinid Fishes across Indian Aquatic Ecosystems: A Comprehensive Review

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Abstract

Indian freshwater carps, barbs and minnows have been classified through successive morphological and molecular frameworks, making the term “cyprinid” taxonomically non-equivalent across historical and modern literature. This review critically evaluates external diagnostic characters, meristics, osteological character complexes, and phylogenetic evidence across Indian riverine, hill-stream, wetland and peninsular faunas. Emphasis is placed on the discriminatory but sometimes homoplastic nature of barbel arrangement, mouth and lip morphology, lateral-line scalation, pharyngeal apparatus, cranial fontanelles, infraorbital bones, Weberian structures and caudal skeleton. Case studies include the *Puntius sensu lato* complex, labeonine genera, *Waikhomia*, *Lepidopygopsis* and the distinct non-cyprinid lineage *Psilorhynchus*. Integrated taxonomic reassessments demonstrate that conspicuous feeding-related modifications are not necessarily synapomorphies, whereas character combinations supported by phylogenomic and voucher-linked data can yield reproducible diagnoses. We distinguish family-level placements under revised Cypriniformes classification from historically broad “Cyprinidae”, and identify where diagnoses reflect autapomorphies, homoplasies, retained ancestral states, or untested proposals. A standardized Indian biodiversity workflow is proposed for voucher acquisition, meristic scoring, cleared-and-stained osteology, imaging, nomenclatural comparison and molecular inference. The available literature supports targeted revision of species-rich groups but does not justify a novel taxonomic rearrangement without new comparative material. This is a comprehensive critical review rather than a newly completed systematic evidence census.

Keywords: Cypriniformes; Cyprinidae; Indian freshwater fishes; comparative osteology; synapomorphy; meristics; taxonomic revision; *Puntius*; *Labeonini*; Western Ghats; DNA barcoding.

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Introduction and nomenclatural scope

Cypriniform fishes are central components of Indian freshwater biodiversity and include economically important carps, stream-associated minnows, and an exceptional array of endemic lineages. Foundational Indian treatments remain valuable for historical distribution, generic concepts and type-linked nomenclature, but identifications cannot simply be transferred to present-day suprageneric classification (Hamilton, 1822; McClelland, 1839; Day, 1878; Talwar and Jhingran, 1991; Menon, 1999; Jayaram, 2010). Modern classifications increasingly recognise several lineages formerly housed within *Cyprinidae sensu lato* as independent families, including *Danionidae*, so a careful review must retain the original author's taxonomic terminology while indicating its current meaning (Stout et al., 2016; Betancur-R. et al., 2017; Tan and Armbruster, 2018).

Our interpretive emphasis is therefore not an exhaustive checklist of Indian fishes but the validity and evidentiary status of characters used to identify taxa and diagnose their evolutionary relationships. A diagnosis is a set of observable features distinguishing a taxon; a synapomorphy is a derived homologous character state supporting a particular clade under an explicit phylogenetic hypothesis. The same feature may provide a useful diagnosis without being a unique shared derived character, especially where convergence is widespread (Mabee et al., 2011; Conway, 2011; Britz and Conway, 2011).

Review approach and evidentiary limitations

A critical narrative synthesis of published through 2024 historical monographs, revisions, comparative anatomy, DNA barcoding studies and phylogenetic analyses was assembled. Priority was assigned to publications supplying explicit diagnoses, vouchers, counts, illustrated skeletal structures, type comparisons or testable trees. No PRISMA record counts, independently screened corpus or pooled effect estimates are claimed. Reference works and regional publications are identified by stable bibliographic records where DOIs are not available. Citations document prior work; proposed matrices and workflows are original syntheses rather than primary observations.

Diagnostic morphology and the problem of character polarity

3.1. Body shape and proportional morphometrics

Standard length, head length, maximum body depth, predorsal distance, caudal-peduncle depth and fin-base lengths are necessary descriptive variables but are influenced by ontogeny, size, sex, nutritional state and habitat. Deep-bodied floodplain barbs and dorsoventrally flattened rheophilic forms demonstrate how similar ecological conditions can favour convergent shapes. Accordingly, morphometric ratios should be paired with appropriate size correction and specimen-level variation rather than treated as immutable species markers (Jayaram, 2010; Kottelat and Freyhof, 2007; Roberts, 1989).

3.2. Scales, lateral line and barbels

Lateral-series scale counts, pored lateral-line scales, predorsal scales, transverse rows and circumpeduncular scales remain integral to field and museum diagnoses, particularly for small barbs. However, lateral-line completeness can differ among lineages and should be scored as a condition rather than collapsed into a present-absent designation. The *Pethia aurea* redescription and the Mizoram *Pethia expletiforis* diagnosis illustrate the value of combinations of lateral-line, pre-dorsal, caudal-peduncle and pigmentation characters (Knight, 2013; Dishma and Vishwanath, 2013; Lalramliana et al., 2014; Shangningam and Vishwanath, 2018).

Rostral and maxillary barbels, the degree of dorsal-ray ossification and serration, and juvenile versus adult patterning proved useful in reconsidering *Puntius* sensu lato. Pethiyagoda et al. (2012) demonstrated that names historically aggregated within *Puntius* encompass multiple morphologically and molecularly differentiated lineages. The subsequent replacement of *Dravidia* by *Haludaria* shows that nomenclature must accompany phylogenetic diagnosis rather than be considered a trivial editorial step (Pethiyagoda, 2013; Katwate et al., 2015).

3.3. Oromandibular structures and feeding-related convergence

Labeonines present pronounced diversity in rostral folds, papillae, lower lip development, keratinized sheaths and adhesive structures. Although such structures can diagnose species and genera, phylogenetic reconstruction suggests repeated origins and reversals, so their occurrence is not automatically evidence of shared ancestry. The multilocus assessment of Yang et al. (2012) rejected the monophyly of some conventionally delimited genera, including *Labeo*, *Garra*, *Bangana*, *Cirrhinus* and *Crossocheilus*. Morphological diagnosis therefore requires evolutionary testing rather than assuming that similarity of mouths reflects closest relationship (Yang et al., 2012; Yang et al., 2010).

Figure 1. Original workflow illustrating why external identification must be connected to comparative osteology, phylogenetics, types and nomenclatural evidence.

Character complex	Standard observation	Strength	Major caution
Lateral line	Number of pored scales; complete/incomplete	Reproducible in preserved material	Damage, stage and counting convention
Barbels	Rostral/maxillary pair counts, length	Diagnostic in some barb groups	Repeated losses and convergence
Dorsal-fin ray	Last unbranched ray; smooth/serrated	Historically important for barbs	Homoplasy and wear
Mouth/lip	Disc, rostral cap, papillae	Strong genus-level descriptive utility	Feeding convergence
Body ratios	SL-normalized measurements	Useful multivariate differentiation	Allometry and preservation
Pigmentation	Blotches, fin markings, juvenile patterns	Practical field identification	Fading and ontogenetic change

Table 1. External morphological characters and their interpretive limitations (author synthesis).

Osteology: homology, synapomorphy and character sampling

Comparative osteology is essential because the distribution of skeletal states often reveals relationships obscured by ecology. Clearing and staining, digital micro-computed tomography and traditional dissection can reveal ossification boundaries, articulations and

structural modifications. However, anatomical terminology must be consistent and character states defined independently of the desired tree. Mabee et al. (2011) explicitly surveyed 62 hyoid and branchial characters across 53 cypriniform taxa; Conway (2011) analysed 127 morphological characters in a broad investigation of Psilorhynchus and related cypriniform lineages. Their outcomes demonstrate both the potential resolution of osteology and the sensitivity of clade support to taxon and character sampling (Mabee et al., 2011; Conway, 2011).

4.1. Neurocranium and circumorbital skeleton

The shape and presence of cranial fontanelles, configuration of the frontals and parietals, supraethmoid region and infraorbital series can yield particularly informative diagnoses. Yet individual bone dimensions are less convincing than homologous articulations or discrete transformations assessed in a defined comparative sample. For Waikhomia, absence of a post-epiphysial fontanelle together with modified frontals, parietals and enlarged infraorbitals formed part of a unique character combination used to distinguish the genus from close relatives (Katwate et al., 2020). These features should not be claimed as individually universal family-level synapomorphies.

4.2. Jaw skeleton, suspensorium and pharyngeal apparatus

Premaxillary and dentary shape, kinethmoid-related articulations, hyomandibular elements, hyoid arch and pharyngeal bones are central to trophic specialization and phylogenetic reconstruction. Oral suction, scraping and benthic feeding create substantial opportunities for convergence. The gill-arch/hyoid character analysis demonstrates why fine-grained osteological states are preferable to broad intuitive character labels such as “sucker mouth” (Mabee et al., 2011; Yang et al., 2012; Stout et al., 2016). Pharyngeal tooth rows and grinding-surface shape should be recorded with wear state, side and ontogeny, rather than treated as independent of diet.

4.3. Vertebral and caudal skeleton

Counts of abdominal and caudal vertebrae, rib associations, supraneurals, neural spines, uroneurals and hypurals can distinguish closely allied forms. In Waikhomia, total vertebral count (30), subdivision into abdominal and caudal series and absence of free uroneural 2 were reported among the diagnostic features, not as newly discovered synapomorphies shared by all Indian cyprinids (Katwate et al., 2020). Accurate axial character coding requires explicit treatment of the Weberian complex and the compound caudal centrum, or counts cannot be compared reliably across studies.

4.4. Weberian apparatus and limits of gross comparisons

The modified anterior vertebrae and Weberian ossicles of otophysans are crucial comparative characters, but they do not by themselves identify Cyprinidae sensu stricto among other otophysans. Investigations of phylogenetic classification use hierarchically nested morphological and molecular evidence; inferring a single skeletal synapomorphy from presence of a shared otophysan complex would be erroneous (Nelson et al., 2016; Betancur-R. et al., 2017; Conway, 2011).

Figure 2. Osteological anatomical regions used for explicit character scoring. Conceptual anatomical index, not a depiction of bones to scale.

Skeletal feature	Possible coding	Application	Caution
Cranial fontanelle	Present / absent; margins	Waikhomia comparative diagnosis	Ontogenetic closure
Infraorbitals	Count, overlap and depth	Genus and species differentiation	Disarticulation artifacts
Gill/hyoid arch	Discrete articulation patterns	Higher-level phylogenetic matrices	Homology definitions essential
Pharyngeal teeth	Rows, formula, crown shape	Species and feeding characterization	Wear and diet convergence
Weberian complex	Ossicles, associated centra	Ostariophysan comparisons	Not exclusive to Cyprinidae
Vertebrae	Precaudal, caudal, total	Species/genera diagnostics	Standardize compound centrum
Caudal	Hypurals and	Character-rich	Fusion and size-

elements

uroneurals

phylogenetic
data

related variation

Table 2. Osteological evidence framework; examples are candidate characters, not asserted universal synapomorphies.

Major Indian taxonomic case studies**5.1. Historical *Puntius* and the revised South Asian barb assemblage**

The former *Puntius* umbrella obscured multiple lineages with distinctive barbels, dorsal spine conditions, lateral-line scale counts and pigmentation. Pethiyagoda, Meegaskumbura and Maduwage (2012) integrated external morphology, osteology and mitochondrial data and proposed recognition of *Dawkinsia*, *Pethia*, *Systemus* and related lineages rather than continued undifferentiated *Puntius* sensu lato. Because some historical names and combinations require subsequent revision, labels on older Indian occurrence surveys should be reconciled against type-linked treatments rather than changed automatically (Pethiyagoda et al., 2012; Kullander, 2008; Kullander and Fang, 2005).

The *Pethia* literature illustrates fine-scale taxonomic differentiation: Knight (2013) disentangled *P. gelius*, *P. canius* and *P. aurea*; Dishma and Vishwanath (2013) diagnosed *P. expletiforis* from the Kaladan drainage; further descriptions and reassessments underscored the need for specimen-level diagnostics and drainage geography (Katwate et al., 2015; Lalramliana et al., 2014; Shangningam and Vishwanath, 2018; Katwate et al., 2018).

5.2. *Waikhomia* and the power of character combinations

Katwate et al. (2020) reassessed Maharaja barbs of the northern Western Ghats and introduced *Waikhomia*. Their diagnosis combined absence of barbels, details of the last unbranched dorsal ray, a complete lateral line of 23–25 pored scales, skull elements, broad infraorbitals, 30 vertebrae, and characters of the caudal skeleton and fin colour. This is a particularly valuable illustration of integrative genus-level diagnosis because no single feature can be assumed unique in a species-rich radiation. It also illustrates why photographs alone are insufficient where diagnostic differences concern cranial and caudal architecture.

5.3. *Lepidopygopsis* and misleading phenetic resemblance

The Periyar endemic *Lepidopygopsis* typus had been interpreted historically as allied to Himalayan schizothoracine fishes owing in part to superficial morphological similarity. Dahanukar et al. (2013) tested this relationship with mitochondrial and nuclear gene evidence and recovered a different affiliation with Asian–African barbin lineages. The outcome is significant for character polarity: the similar scale sheath around the anal-fin base could reflect retained ancestry or independent evolution rather than a reliable schizothoracine synapomorphy. Morphological resemblance, even when historically persuasive, must be tested against alternative tree hypotheses.

5.4. Labeonines: the limits of oral morphology

In the Labeonini, morphological specialization around the mouth has encouraged broad generic assignments. Yang et al. (2012), using five mitochondrial and four nuclear markers, recovered non-monophyly of multiple conventional genera and proposed revised tribal subdivisions. These findings do not invalidate external characters for species identification; rather, they demonstrate that character utility for identification and character support for phylogeny must be evaluated separately. The use of mouth architecture alone to define a genus risks grouping unrelated organisms that share feeding modes (Yang et al., 2012; Yang et al., 2010).

5.5. *Psilorhynchus* and boundary testing outside Cyprinidae sensu stricto

Torrent minnows *Psilorhynchus* occupy fast-flowing Indo-Burmese and peninsular waters but are assigned to *Psilorhynchidae* rather than treated indiscriminately as *Cyprinidae*. The osteological synthesis by Conway (2011) remains a model of regionally relevant comparative work: extensive species sampling allowed assessment of derived and homoplastic character states, and clarified phylogenetic placement within *Cypriniformes* under a specified analytical framework. Its inclusion here serves to test the boundary of historical “cyprinid-like” morphology, not to relabel *Psilorhynchus* as a cyprinid.

Figure 3. Original schematic of integrative reassessment in broad historical generic complexes; the diagram is not a reconstructed phylogeny.

Taxon/problem	Evidence used in key study	Reassessment	Central lesson
<i>Puntius</i> s.l.	Morphology, osteology, mitochondrial markers	Multiple generic lineages	Historic broad genus was heterogeneous
<i>Waikhomia</i>	Cranium,	Distinct	Character

	vertebrae, external features, integrative data	western-Ghats genus	combinations strengthen diagnosis
Lepidopygopsis	Mitochondrial and nuclear phylogenetics	Rejected presumed schizothoracine affinity	Similarities can be non- synapomorphic
Labeonini	Mitochondrial + nuclear phylogeny	Several historical genera non- monophyletic	Mouth forms often convergent
Pethia complexes	Meristics, spine and colour patterns	Species-level revision	Name changes require type comparison
Psilorhynchus	127-character osteological phylogeny	Placement within Cypriniformes	Family boundaries require explicit testing

Table 3. Evidence-led Indian and South Asian systematic case studies (Pethiyagoda et al., 2012; Yang et al., 2012; Conway, 2011; Dahanukar et al., 2013; Katwate et al., 2020).

Aquatic ecosystem contexts and sampling bias

The Ganga–Brahmaputra network, Himalayan foothill torrents, northeastern interbasin drainages, peninsular rivers, lateritic streams and Western Ghats headwaters differ in flow regime, substrate, elevation and historical connectivity. These differences influence both morphological adaptation and accessibility of samples. Historical inventories by Hamilton (1822), Day (1878), Talwar and Jhingran (1991) and Jayaram (2010) are necessary points of nomenclatural comparison but have different coverage, species concepts and detection effort. Modern localized descriptions should therefore be reconciled against both basin geography and the chronology of taxonomic revision (Knight, 2013; Dishma and Vishwanath, 2013; Katwate et al., 2020).

Collections concentrated on major rivers or market fishes can underrepresent short endemic headwater forms. Miniaturized cypriniforms also complicate character scoring because some structures are reduced or developmentally retained; comparative osteology of *Paedocypris* and *Danionella* shows that skeletal reduction and novelty can be phylogenetically informative without translating into a simple universal body-size rule (Rüber et al., 2007; Britz and Conway, 2009; Britz et al., 2009). Regional inventories and molecular reference panels must retain locality, drainage, adult size and voucher metadata.

Molecular systematics and integrative delimitation

DNA barcoding offers an efficient quality-control layer for identification, particularly where juvenile and cryptic forms cannot confidently be separated by gross morphology. However, the COI locus is a maternal marker and may mislead in cases of introgression, incomplete lineage sorting, mislabelled databases or inadequate geographic representation. Indian data documented substantial identification success but also a problematic subset requiring taxonomic reassessment (Chakraborty and Ghosh, 2014, 2015). This finding accords with fish barcoding experience elsewhere and emphasizes curated reference vouchers (Hebert et al., 2003; Ward et al., 2005; Ward et al., 2009; Hubert et al., 2008).

Multiple unlinked nuclear loci or genomic datasets are increasingly important when questions involve deeper relationships and monophyly of historical genera. The anchored-enrichment analysis of Stout et al. (2016) illustrates family-level restructuring, while Yang et al. (2012) addresses the Labeonini at finer taxonomic resolution. Molecular trees must still be tested for sampling gaps, paralogy, hybridization and outgroup sensitivity; molecular support is not a substitute for diagnoses of specimens accessible to future researchers.

Distinguishing diagnostics, synapomorphies, autapomorphies and homoplasy

Diagnostic combinations may be sufficient for practical species recognition without supplying unique evolutionary innovations. A synapomorphy is an inferred shared derived condition mapped onto an explicit genealogy; an autapomorphy is derived but confined to a terminal lineage, while homoplasy includes independent origin or reversal. The labeonine mouth illustrates homoplastic repetition, and *Lepidopygopsis* demonstrates the hazards of interpreting superficial resemblance as relationship (Yang et al., 2012; Dahanukar et al., 2013). Osteological analyses with enumerated character states are necessary to test these alternatives (Conway, 2011; Mabee et

al., 2011).

Term	Operational meaning	Acceptable claim	Unacceptable shortcut
Diagnosis	Differential combination of features	Specimens can be distinguished	Each character is evolutionarily unique
Synapomorphy	Homologous shared derived state	Supports specified clade on a tree	Any shared feature means close relationship
Autapomorphy	Unique derived feature of a terminal	May distinguish a taxon	Demonstrates relationship with another terminal
Symplesiomorphy	Shared ancestral state	Retained ancestral similarity	Unambiguous evidence of a subgroup
Homoplasy	Independent gain or reversal	Conflicting or convergent signal	All characters with conflicting trees are errors

Table 4. Taxonomic terminology and inferential safeguards.

Recommended standardization of Indian cyprinid revisionary studies

Future surveys should preserve field colour photographs, standardized geographic coordinates, habitat descriptions, date, collection permission and specimen-level unique identifiers. Minimum morphological records should include standardized SL-based measurements, complete fin-ray and scale-series definitions, sex and stage where known, and examination of several individuals representing different populations. Skeletal preparations should document fixation and clearing method, imaging scale, orientation, the number of dissected specimens and all alternative observed states. Character matrices should be archived with unambiguous definitions and linked specimen vouchers (Mabee et al., 2011; Kottelat and Freyhof, 2007; Tan and Armbruster, 2018).

Taxonomic proposals require comparison with validly named type specimens or high-quality documented type representations and compliance with zoological nomenclatural rules. For geographically isolated putative species, repeated sampling and an explicitly defined delimitation criterion are preferable to single-individual genetic distances. Databases such as the Catalog of Fishes and FishBase are useful navigation tools, but their content is periodically revised and should not override original descriptions or the nomenclatural code (Jayaram, 2010).

Conservation relevance of sound taxonomy

Unresolved synonymy and cryptic species complexes can distort estimates of endemism, abundance, threatened status and fishery identity. Misidentification is consequential in Indian hotspots where small drainage-restricted species can be confused with widespread names. The reassessment of *Lepidopygopsis* and Western Ghats barbs demonstrates why historical biogeography and conservation planning depend on correct evolutionary placement, while *Pethia* revisions show how species boundaries can remain confused even among relatively accessible fishes (Dahanukar et al., 2013; Katwate et al., 2020; Knight, 2013).

Research gaps and future directions

Priority gaps include inadequate osteological material for several regional genera, inconsistencies in counting conventions, uneven representation of peninsular and northeastern tributaries in molecular datasets, and weak integration of type-based diagnoses with genomic ancestry. Comparative studies should predefine alternative phylogenetic hypotheses, include developmentally staged skeletons, report uncertainties around character states, and explicitly test effects of ecological convergence. The highest-value advances would be open specimen-linked image archives, multi-institutional osteological atlases and revisable morphological matrices tested against sequence-supported phylogenies (Mabee et al., 2011; Stout et al., 2016; Katwate et al., 2020).

Conclusions

The taxonomy of Indian cypriniform fishes has shifted from broad external-morphology arrangements toward lineage-aware classifications informed by comparative skeletal anatomy and molecular evidence. For practical identification, characters such as scales, fin rays, barbels, oral folds and colour remain indispensable, yet their evolutionary interpretation requires explicit homologous-

state comparisons and phylogenetic optimization. Indian case studies of *Puntius*, *Pethia*, *Waikhomia*, *Lepidopygopsis* and *Labeonini* establish the scientific value of integrative revision and demonstrate that oral or body-shape resemblance can conceal deeper evolutionary differences. Future work should retain historically traceable names, voucher-linked diagnoses, detailed skeletal documentation and well-sampled phylogenetic analyses. No new species synonymy or family placement is proposed here without primary character and molecular data.

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