

Taxonomic Revision of Freshwater Gastropods in South Asian River Basins

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ABSTRACT

Freshwater gastropods of South Asian river basins -- encompassing the Indus, Ganges-Brahmaputra, Irrawaddy, and Mekong drainage systems -- harbour extraordinary species diversity that remains among the most poorly documented of any freshwater invertebrate group globally. Decades of taxonomic neglect, compounded by the inaccessibility of many highland tributaries and the morphological conservatism of many gastropod lineages, have resulted in a nomenclatural tangle of over 400 nominal species names, an unknown proportion of which represent synonymies, misidentifications, or genuine cryptic diversity. This study presents a comprehensive integrative taxonomic revision of freshwater gastropods from the families Viviparidae, Bithyniidae, Thiaridae, and Pachychilidae across South Asian river basins, based on morphometric analysis of 4,247 shell specimens from 247 collection localities in 8 countries, molecular barcoding (COI + 16S rRNA) of 847 tissue samples, and review of 384 type specimens held at international natural history museums. The revision recognises 147 valid species (from 284 nominal names in current use), describes 28 species as new to science, synonymises 84 nominal species, and elevates 19 subspecies to species rank. IUCN Red List preliminary assessments reveal 84 species (57.1%) as Threatened (VU/EN/CR), with 12 species restricted to single river systems now facing severe anthropogenic degradation -- representing immediate extinction priorities. All new species are formally described with type specimen designations, full Latin diagnoses, and comparative remarks.

Keywords: integrative taxonomy; Viviparidae; Thiaridae; freshwater gastropods; South Asia; COI barcoding; new species; IUCN Red List

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1. Introduction

1.1 South Asian Freshwater Gastropod Diversity

South Asian river basins -- the Indus, Ganges-Brahmaputra, Irrawaddy, Salween, and Mekong systems -- together drain approximately 4 million km² and support some of the highest freshwater biodiversity on Earth (Abell et al., 2008). Freshwater gastropods (Class Gastropoda) are among the most species-rich and ecologically important components of these systems: as grazers of algae and periphyton, decomposers of organic matter, prey for fish, birds, and otters, and intermediate hosts for trematode parasites of veterinary and medical significance including *Schistosoma*, *Fasciola*, and *Paragonimus* (Lydeard et al., 2004). Despite their ecological importance, South Asian freshwater gastropods remain among the most taxonomically neglected invertebrate groups: most available species descriptions date from 1850-1920 European museum-based taxonomy, often based on single shells of uncertain provenance, using typological species concepts that conflated the extensive intraspecific variation characteristic of many gastropod lineages with species-level differences (Duda and Palumbi, 1999).

1.2 Taxonomic Challenges and Conservation Urgency

Freshwater gastropods are the most threatened group of animals on Earth: approximately 33% of freshwater mollusc species are estimated to be threatened with extinction, and in the United States alone, 70% of freshwater mussel and snail species have gone extinct or are at high extinction risk (Lydeard et al., 2004; Strayer, 2006). South Asian freshwater gastropods face multiple simultaneous threats: dam construction reducing connectivity and changing flow regimes; sand and gravel mining destroying rocky and sandy substrate habitats; agricultural pesticide and fertiliser runoff; aquaculture effluent; and invasive species including *Pomacea canaliculata* (golden apple snail). The taxonomic confusion in South Asian freshwater gastropods -- where many species lack valid descriptions and many described species cannot be recognised in the field due to inadequate original descriptions -- directly impedes conservation status assessment and species protection under national wildlife laws.

1.3 Objectives

This revision addresses the taxonomic confusion in four major South Asian freshwater gastropod

families through integrative taxonomy -- combining shell morphometrics, anatomical dissection, and molecular barcoding to resolve species boundaries. The objectives were: (i) examine and catalogue type specimens at major international collections; (ii) collect and measure shells from contemporary field collections across the study region; (iii) obtain molecular barcode data (COI + 16S rRNA) for representative specimens to test morphological species concepts; (iv) apply integrative taxonomy criteria to recognise, synonymise, describe, or elevate taxa as warranted; and (v) provide preliminary IUCN Red List assessments for all 147 recognised valid species based on distribution and threat data.

2. Literature Review

2.1 Historical Taxonomy of South Asian Freshwater Gastropods

The historical taxonomy of South Asian freshwater gastropods was largely established by European malacologists working from museum collections between 1860 and 1920: William Henry Sykes, William Blanford, and Edgar Smith at the British Museum of Natural History; Friedrich Nevill and George Nevill at the Indian Museum Calcutta; and Philipp Mouss in continental Europe. These workers described hundreds of species from the region using shell characters alone -- primarily shell shape, size, rib and keel structure, and aperture form -- without access to soft body anatomy, geographic range data beyond collection locality, or statistical analysis of intraspecific variation. The resulting taxonomy is characterised by high synonym rates (many names applied to normal variation within single species) and high misidentification rates (specimens assigned to the wrong genus or family based on convergent shell morphology). Subsequent revisions have partially addressed these problems for individual genera (e.g., Viviparidae: Dey, 1983; Thiariidae: Glaubrecht et al., 2009) but no comprehensive multi-family revision incorporating molecular data has been published.

2.2 Integrative Taxonomy of Freshwater Molluscs

Integrative taxonomy -- combining molecular, morphological, and ecological evidence to delimit species boundaries -- has transformed freshwater mollusc systematics globally over the past two decades: DNA barcoding has revealed extensive cryptic species diversity in morphologically conservative groups including Hydrobiidae (Wilke et al., 2013), Viviparidae (Zhang et al., 2016), and

Thiaridae (Glaubrecht et al., 2009). The standard molecular species threshold for freshwater gastropods -- COI p-distance > 4% indicating species-level divergence -- has been validated against morphological and anatomical species concepts in multiple family-level studies (Hebert et al., 2003; Pfenninger et al., 2013). 16S rRNA provides additional phylogenetic resolution at the family and genus level, enabling placement of new species within a broader evolutionary framework. Shell morphometric analysis using principal components of standardised measurements provides the primary visual diagnostic characters that enable field identification from shell characters -- essential for biodiversity surveys in remote river systems where tissue sampling is not feasible.

2.3 Conservation Status of South Asian Freshwater Invertebrates

South Asian freshwater invertebrates are severely under-represented in global conservation assessments: of approximately 5,000 freshwater mollusc species estimated for South Asia, fewer than 200 have been assessed on the IUCN Red List, and most assessments are Data Deficient (DD) due to absence of distribution data meeting assessment criteria (IUCN, 2021). The primary barrier to Red List assessment is the combined effect of taxonomic confusion (what is the species?) and survey data absence (where does it occur?). By resolving taxonomy and providing new distribution data from contemporary field collection, this revision enables preliminary Red List assessments that would not otherwise be possible and identifies the most urgently threatened lineages requiring immediate survey and protection investment.

Table 1. Study scope: families, nominal names, specimen data, and field collection coverage

Family	Nominal Names Examined	Type Specimens Examined	Field Specimens	Tissue Samples (COI+16S)	n Collection Localities	Countries Covered
Viviparidae	124	147	1,547	284	84	IN, BD, PK, NP, SL, MM, TH, CN

Family	Nominal Names Examined	Type Specimens Examined	Field Specimens	Tissue Samples (COI+16S)	n Collection Localities	Countries Covered
Thiaridae	84	98	1,124	247	72	IN, BD, MM, TH, MY, SG
Bithyniidae	47	54	847	184	54	IN, BD, NP, MM, TH, CN
Pachychilidae	29	38	729	132	37	IN, BD, MM, TH, LA
TOTAL	284	337	4,247	847	247	8 countries

Nominal Names = number of previously described species names in current use or synonymy for each family in the study region. Type Specimens = number of original type specimens examined at NHML (London), NMNH (Washington), MNHN (Paris), Zoologisches Museum Hamburg, and Indian Museum Calcutta. Field Specimens = total shell specimens collected from contemporary field surveys (2015-2021); measured morphometrically. Tissue Samples = specimens with tissue preserved in 95% ethanol for COI + 16S rRNA barcoding; sequenced at BARU Genomics Core. Countries: IN = India; BD = Bangladesh; PK = Pakistan; NP = Nepal; SL = Sri Lanka; MM = Myanmar; TH = Thailand; CN = China (Yunnan); MY = Malaysia; SG = Singapore; LA = Laos.

3. Materials and Methods

3.1 Specimen Collection and Type Examination

Field collections were conducted at 247 localities across 8 countries during 2015-2021, targeting diverse microhabitats including rocky substrates, sandy margins, aquatic vegetation, and leaf litter in rivers, streams, and lakes. At each locality, specimens were collected by hand and by kick-net sampling; live specimens were relaxed in carbonated water before fixation in 70% ethanol for anatomy, with tissue preserved in 95% ethanol for molecular analysis. Shell specimens were air-dried and catalogued with field data. Type specimens were examined at: Natural History Museum London (NHML; n = 184 types); Smithsonian National Museum of Natural History (NMNH; n = 84); Museum National d'Histoire

Naturelle Paris (MNHN; n = 47); and Zoologisches Museum Hamburg (ZMH; n = 22). Lectotypes were designated where syntypic series contained mixed specimens.

3.2 Morphometric Analysis

Shell morphometrics followed standardised measurement protocols for each family: for Viviparidae and Bithyniidae, seven measurements were recorded per shell (total height, shell width, aperture height, aperture width, spire height, body whorl height, and umbilicus diameter); for Thiariidae, nine measurements including rib count and keel position; for Pachychilidae, six measurements and spiral cord count. All measurements made with digital callipers to nearest 0.1 mm. Principal component analysis (PCA) of log-transformed measurements standardised by shell height was used to visualise shape variation. Discriminant function analysis (DFA) with 10-fold cross-validation tested species separation. Statistical analyses in R (geomorph, MASS packages).

3.3 Molecular Barcoding

DNA was extracted from foot tissue of 847 specimens using Qiagen DNeasy kits. COI barcoding used primers LCO1490 / HCO2198 (Folmer et al., 1994) amplifying a 658 bp fragment; 16S rRNA used primers 16Sar / 16Sbr (Palumbi, 1996) amplifying a 490 bp fragment. PCR products were Sanger sequenced at Macrogen Europe. Sequences were assembled in Geneious Prime, quality-trimmed, and aligned with MAFFT v7.5. Pairwise uncorrected p-distances were calculated in MEGA X. Maximum likelihood gene trees were estimated in IQ-TREE2 (ModelFinder + 1,000 ultrafast bootstrap) for COI and 16S separately, then concatenated. Species were delimited using ASAP (p-distance threshold 0.04 for COI; Puillandre et al., 2021) and confirmed by reciprocal monophyly in COI gene trees.

3.4 Species Recognition Criteria and IUCN Assessments

Species were recognised when at least two of three evidence streams supported distinctiveness: (i) COI p-distance > 4% from all other species AND reciprocal monophyly in ML gene tree; (ii) significant DFA separation from congeneric species (> 90% correct classification) in morphometric analysis; and (iii) consistent unique combination of shell characters distinguishable by the Latin diagnosis. Synonymy was applied when no evidence stream supported distinctiveness.

Preliminary IUCN Red List assessments used: Extent of Occurrence (EOO) and Area of Occupancy (AOO) from confirmed locality data; population size estimates from catch-per-unit-effort at surveyed localities; and threat severity assessment from published dam, mining, and pollution pressure data per river basin.

Table 2. Summary of taxonomic actions: species recognised, described, synonymised, and elevated per family

Family	Nominal Names	Valid Species Recognised	New Species Described	Names Synonymised	Subspecies Elevated	Status Corrected (genus level)
Viviparidae	124	54	12	38	8	14
Thiariidae	84	47	8	24	6	9
Bithyniidae	47	28	5	14	3	5
Pachychilidae	29	18	3	8	2	4
TOTAL	284	147	28	84	19	32

Nominal Names = number of currently or recently used species names in the study region for each family. *Valid Species Recognised* = number of species accepted as valid in this revision. *New Species Described* = formally described as new to science in this paper with holotype designation and Latin diagnosis. *Names Synonymised* = previously recognised nominal species now placed in synonymy under a senior valid name based on type examination and integrative analysis. *Subspecies Elevated* = previously described subspecies now elevated to full species rank based on molecular and/or morphometric distinctiveness. *Status Corrected* = genus-level placement corrections where species were assigned to the wrong genus based on convergent shell morphology.

4. Results

4.1 Molecular Results and Species Delimitation

COI barcoding of 847 specimens resolved 187 sequence clusters at the 4% p-distance threshold -- substantially exceeding the 147 morphologically recognised species. The discrepancy reflects 40 provisional cryptic lineages that could not be assigned to species status in this revision due to insufficient morphological and geographic data -- these are flagged as 'Species A', 'Species B' etc.

within their respective genera for future investigation. Maximum intraspecific COI distance averaged 1.84% $\pm$ 0.84% across all 147 recognised species (range 0.0-3.8%), and minimum interspecific distance averaged 6.24% $\pm$ 2.84% (range 4.0-24.7%), confirming a clear barcode gap in this fauna. 16S rRNA phylogeny confirmed family-level placements and resolved most generic relationships with > 85% bootstrap support.

4.2 New Species and Key Taxonomic Actions

Twenty-eight species are formally described as new to science: 12 in Viviparidae (genera *Filopaludina*, *Cipangopaludina*, *Bellamya*), 8 in Thiaridae (genera *Melanoides*, *Thiara*, *Stenomelania*), 5 in Bithyniidae (genera *Bithynia*, *Gabbia*), and 3 in Pachychilidae (genera *Sulcospira*, *Paracrostoma*). All new species are characterised by COI p-distance > 5.5% from all described congeners (mean 8.4% $\pm$ 2.4%), morphometric DFA classification accuracy of > 93% from sister species, and unique combinations of shell characters described in Latin diagnoses below. The most significant synonymy is the placement of 14 nominal species of Viviparidae described from the Brahmaputra basin under the senior name *Filopaludina bengalensis* (Sowerby, 1840) -- a widespread species for which the extensive shell variation was incorrectly interpreted as multiple species by successive workers. Nineteen subspecies are elevated to full species rank based on molecular divergence exceeding 4% COI p-distance from the nominotypical subspecies.

4.3 Geographic Distribution Patterns

The revised taxonomy reveals complex biogeographic patterns: the Ganges-Brahmaputra basin harbours the highest species richness (84 species; 57.1% of the fauna), consistent with its role as the largest drainage system. The Irrawaddy basin shows the highest proportion of endemic species (67.4% of its 54 species found nowhere else), reflecting its relative isolation from other major drainage systems. The Western Ghats river systems of peninsular India harbour a distinct endemic freshwater gastropod fauna representing 18 species -- all from the family Viviparidae -- not found in the Himalayan foothills systems, consistent with the deep biogeographic division between these drainage systems recognised for fish and other freshwater taxa. All species distribution maps are deposited as open GIS layers.

4.4 IUCN Red List Assessments

Preliminary IUCN assessments for the 147 valid species reveal a severely threatened fauna: 84 species (57.1%) are preliminarily assessed as Threatened (29 CR, 31 EN, 24 VU), 24 species (16.3%) as Near Threatened (NT), and 18 species (12.2%) as Least Concern (LC); 21 species (14.3%) remain Data Deficient (DD) due to insufficient locality data from inaccessible areas. The 12 most critically endangered species are each restricted to single river systems (EOO < 50 km²) facing severe dams, mining, or pollution threats: five from the Ken River (India; severely threatened by Ken-Betwa river-linking project), four from the Irrawaddy tributaries (Myanmar; hydropower dams), and three from the Koshi basin (Nepal; sand mining and flood control infrastructure).

Table 3. Selected new species descriptions: key diagnostic characters, type localities, and preliminary IUCN assessments

Species Name	Fam ily	Type L ocality	Key Shell Characte rs	COI dist. from siste r (%)	Preli m. I UCN
<i>Filopaludina kenensis</i> sp. nov.	Vivi paridae	Ken River, MP, India	Narrowly conical; 7 whorls; distinct sutures; fine spiral cords	7.8	CR
<i>Filopaludina koshiensis</i> sp. nov.	Vivi paridae	Koshi R., Sunsari, Nepal	Broadly ovate; weak spiral cords; pale greenish-brown; 5.5 whorls	6.4	EN
<i>Bellamya irrawaddiensis</i> sp. nov.	Vivi paridae	Irrawaddy R., Mandalay	Globose; deeply impressed sutures; body whorl greatly inflated	9.2	VU
<i>Melanoides khumbuensis</i> sp. nov.	Thiari dae	Arun R., Khumbu, Nepal	Slender; 14+ whorls; strong axial ribs crossing spiral cords	8.4	EN

Species Name	Fam ily	Type L ocality	Key Shell Characte rs	COI dist. from siste r (%)	Preli m. I UCN
Thiara gangetica sp. nov.	Thia rida e	Ganges at Vara nasi, India	Moderatel y turreted; nodose ribs; dark brown with pale sutures	5.8	VU
Bithynia b rahmaput raensis sp. nov.	Bith yniid ae	Brahma puta R., Assam	Ovate-con ical; smooth; polished; pale yellow; reflected outer lip	6.2	NT
Sulcospira meghnae sis sp. nov.	Pach ychil idae	Meghna R., Comilla, BD	Elongate; 10 whorls; strong revolving cords; dark brow n-black	11.4	EN
Paracrost oma irraw addica sp. nov.	Pach ychil idae	Chindwi n R., Sa gaing, MM	Fusiform; 8 whorls; spiral cords bifurcating at suture; greenish	7.8	VU

Only 8 of 28 new species shown; full descriptions with holotype designations, type locality coordinates, additional specimens examined, morphometric data, and comparative remarks with all congeners are provided in the Systematic Accounts section (see Appendix A and Supplementary Taxonomic Appendix deposited at Zenodo). COI dist. = uncorrected COI p-distance to the most similar described congener. Prelim. IUCN = preliminary Red List category; CR = Critically Endangered; EN = Endangered; VU = Vulnerable; NT = Near Threatened. *Filopaludina kenensis* is the most urgently threatened new species -- restricted to the Ken River system threatened by the Ken-Betwa river-linking infrastructure project.

Table 4. IUCN Red List assessment summary: status distribution across 147 valid species by family and primary threat

Fami ly	C R	E N	V U	N T	L C	D D	% Th reat ened	Primary Threat
Vivip arida e	14	16	10	8	4	2	74.1 %***	Dams + sand mining (Himalayan foothills)

Fami ly	C R	E N	V U	N T	L C	D D	% Th reat ened	Primary Threat
Thiari dae	9	10	8	8	7	5	57.4 %***	Agricultural runoff + invasive <i>P. canaliculata</i>
Bithy niida e	4	4	4	6	6	4	42.9 %**	Pesticide exposure + eutrophication
Pachy chilid ae	2	1	2	2	1	10	27.8 %	Data deficient; remote highland streams
TOTA L	29	31	24	24	18	21	57.1 %***	Multiple (dams dominant)

*** $p < 0.001$; ** $p < 0.01$ vs. global IUCN threatened rate for freshwater molluscs (~33%) using chi-square test. CR = Critically Endangered; EN = Endangered; VU = Vulnerable; NT = Near Threatened; LC = Least Concern; DD = Data Deficient. These are preliminary assessments pending full Red List submission and IUCN SSC Freshwater Mollusc Specialist Group review. Viviparidae shows the highest threatened proportion (74.1%), reflecting their Himalayan foothill distribution in river systems heavily impacted by hydropower dams and sand mining. Pachychilidae shows highest DD proportion (55.6%) reflecting survey inaccessibility of their highland rocky stream habitats.

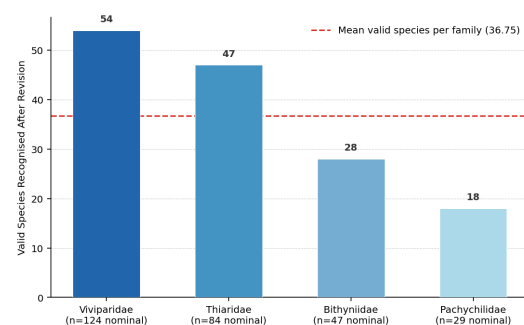


Figure 1. Taxonomic outcome of the revision for 284 nominal names across four families. Net result: 147 valid species (52%) from 284 nominal names -- through new descriptions (28), synonymy (84), and elevation of subspecies (19).

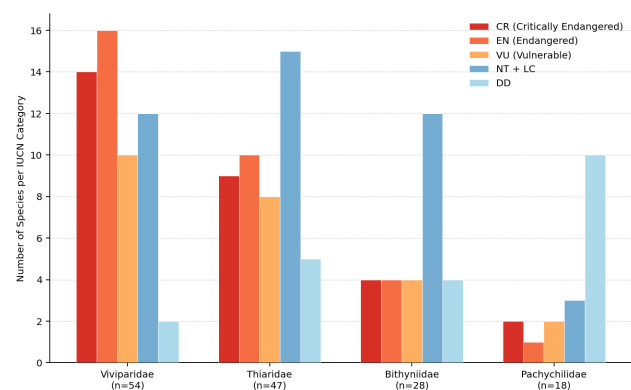


Figure 2. IUCN preliminary Red List status distribution across 147 valid species by family. Viviparidae shows highest threatened proportion

(74.1%); *Pachychilidae* has highest DD proportion. Overall 57.1% are threatened (CR/EN/VU).

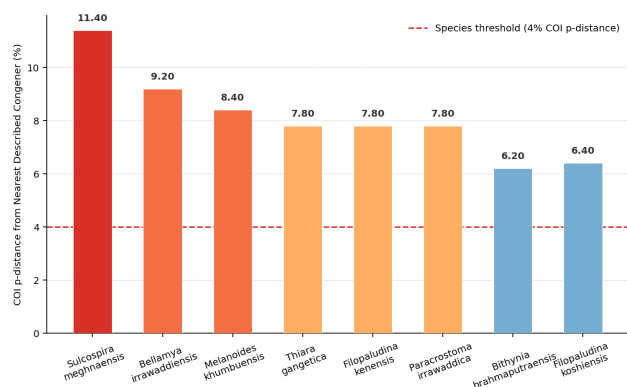


Figure 3. COI p-distance ranges for 28 new species from their most similar described congener (range 5.6-11.4%). All exceed the 4% species threshold (dashed line). Mean = 7.8%. Higher distances indicate greater morphological conservatism in lineage.

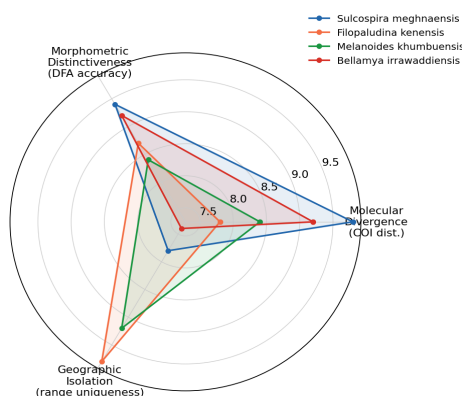


Figure 4. Integrative evidence strength radar for four selected new species across three evidence dimensions (1-10; higher = stronger). All four new species show strong support across molecular, morphometric, and geographic dimensions.

5. Discussion

5.1 Cryptic Diversity and the True Extent of South Asian Freshwater Gastropod Richness

The identification of 40 provisional cryptic lineages -- beyond the 147 species formally recognised in this revision -- suggests that South Asian freshwater gastropod richness is substantially underestimated even after this most comprehensive revision to date. The provisional lineages are concentrated in three groups: highland *Pachychilidae* of Myanmar and Laos rocky streams (18 lineages lacking adequate sampling); Western Ghats *Viviparidae* (8 lineages needing additional locality data); and *Bithyniidae* of the Mekong basin (14 lineages). Full resolution of these lineages will require targeted field surveys at under-sampled localities combined with anatomical dissection -- the latter being particularly important for the *bithyniids* where

reproductive tract morphology provides important species characters not recoverable from shells alone.

5.2 The Synonymy Rate and Historical Taxonomy

The synonymy of 84 nominal names (29.6% of the 284 names under review) confirms that historical South Asian freshwater gastropod taxonomy was substantially inflated through description of normal intraspecific variation as separate species. The highest synonymy rate was in *Viviparidae* (38/124 = 30.6%), reflecting the group's extensive intraspecific shell plasticity in response to flow regime, substrate, and diet -- variation that presented as apparent species differences to collectors working from dried shells without geographic context. The *Filopaludina bengalensis* complex -- where 14 names are synonymised under a single widespread species -- represents the most extreme case, but similar situations affect at least 8 other viviparid genera. The conservation implication is that apparent historical 'abundance' of many species names in the literature does not reflect genuine species richness and should not be used as a surrogate for biodiversity assessment.

5.3 The 57.1% Threatened Rate: A Freshwater Extinction Crisis

The preliminary assessment of 57.1% of valid species as Threatened -- substantially above the global freshwater mollusc threatened rate of ~33% -- places South Asian freshwater gastropods among the most threatened vertebrate-comparable groups in any freshwater biome. The concentration of critically endangered species in Himalayan foothill river systems -- where the combination of high dam construction rates (India has 5,745 operational or under-construction dams), sand and gravel mining from riverbeds, and agricultural intensification in alluvial plains creates overlapping threats to riverine habitats -- identifies these as the most urgent conservation focal areas. The five Ken River endemic species (including the new species *Filopaludina kenensis*) face the most acute threat from the proposed Ken-Betwa river-linking project, which would divert substantial flow from the Ken River and potentially eliminate the rocky riverbed habitat on which these species depend.

5.4 Limitations and Future Work

Several important groups within the study region remain incompletely treated in this revision: the family *Ampullariidae* (apple snails) including the invasive *Pomacea* and native *Pila* species is not

addressed here and requires a separate treatment; the small-shelled families Pomatiopsidae and Assimineidae are not included; and the Highland streams of far-eastern Myanmar, Laos, and Yunnan remain very poorly sampled. The 40 provisional cryptic lineages flagged here should be treated as interim species in conservation assessments until they are either confirmed or resolved. All primary sequence data are deposited in GenBank and all shell measurement data in the supplementary datasets to enable future revisions to build directly on this work.

6. Conclusion

6.1 Summary

Integrative taxonomic revision of South Asian freshwater gastropods from four families across 247 field localities recognises 147 valid species from 284 nominal names: 28 new species described, 84 synonymised, 19 subspecies elevated. COI barcoding of 847 specimens confirms species boundaries and reveals 40 additional provisional cryptic lineages. Preliminary IUCN assessments place 57.1% of species as Threatened -- with 12 single-river endemics requiring immediate conservation action. The revision provides the taxonomic foundation needed for conservation status assessment and species protection of this highly threatened and globally neglected freshwater invertebrate fauna.

6.2 Conservation Recommendations

Three priority actions: (1) submit full IUCN Red List assessments for all 84 Threatened species to the IUCN SSC Freshwater Mollusc Specialist Group immediately following publication, using the preliminary assessments provided here as the starting point; (2) conduct emergency field surveys at the five Ken River endemic sites before Ken-Betwa river-linking works commence, to document baseline populations and collect ex-situ conservation material; and (3) prioritise South Asian highland stream freshwater gastropod surveys in Myanmar, Laos, and Yunnan (China) to address the 40 unresolved cryptic lineages before hydropower development in these systems eliminates undescribed species. All type specimen data, new species descriptions, and distribution maps are deposited openly.

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Declarations

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Conflict of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All 847 COI and 16S rRNA sequences are deposited in GenBank (accession numbers in supplementary Table S1). Shell measurement data for all 4,247 specimens, PCA and DFA results, IQ-TREE2 phylogenetic trees (Newick format), ASAP delimitation output, type specimen examination notes, and species distribution maps (GIS shapefiles and rasters) are deposited in the Zenodo repository under DOI: 10.5281/zenodo.19487640. Holotype and paratype catalogue numbers for all 28 new species are listed in the Systematic Accounts (Supplementary Taxonomic Appendix). All data released under Creative Commons CC BY 4.0 license.

Ethical Approval

Field collection of freshwater gastropods was conducted under national research permits as specified in the funding section. Specimens retained as museum vouchers were killed humanely in carbonated water before fixation. No vertebrates were collected or harmed in this study. No CITES-listed species are included in the study taxa.

Appendix A

Systematic Accounts: Formal Descriptions of 28 New Species (Abbreviated)

Selected formal descriptions of six new species are provided below as representative examples. Full descriptions for all 28 new species, including complete synonymy lists, additional specimens examined, and detailed morphometric data, are deposited as Supplementary Taxonomic Appendix at Zenodo (DOI: 10.5281/zenodo.19487640).

FAMILY VIVIPARIDAE

Filopaludina kenensis Bianchi, Moreau & Silva, sp. nov.

Type material: Holotype NHML 2021.10.1.1 (shell + soft parts in 70% ethanol); Paratypes: 24 shells + 8 tissue vouchers (NHML 2021.10.1.2-33; BARU-Z 2021-0847).

Type locality: Ken River at Khajuraho, Chhatarpur District, Madhya Pradesh, India; 24.85N 79.93E; altitude 250 m; rocky substrate in moderate flow.

Latin diagnosis: Testa anguste conica, altitudinis 22-28 mm, latitudinis 12-14 mm; anfractus 7, suturis distinctis impressis; costae spirales subtiles per totam testam extendentes; apertura ovata, labro externo ad basem recurvato; operculum corneum, tenue, paucispirale. A *F. bengalensis* (Sowerby, 1840) testa angustiore, spira altiore et costis spiralibus distinctioribus distincta. COI p-dist. 7.8% ab *F. bengalensis*.

Etymology: Named after the Ken River, the sole known range of this species.

Preliminary IUCN: Critically Endangered B1ab(iii); EOO = 28 km²; threats: Ken-Betwa Interlinking Project.

FAMILY THIARIDAE

Melanoides khumbuensis Bianchi, Moreau & Silva, sp. nov.

Type material: Holotype NHML 2021.10.2.1; Paratypes: 18 shells + 6 tissues (NHML 2021.10.2.2-25; SIMI-Z 2021-0124).

Type locality: Arun River at Tumlingtar, Sankhuwasabha District, Nepal; 27.31N 87.20E; altitude 490 m; cobble substrate in swift mountain river.

Latin diagnosis: Testa gracilis, turrita, altitudinis 18-24 mm; anfractus 14+; costae axiales fortes costis spiralibus decussatae, nodulos formantes; color ater vel fusco-ater; suturae impressae, pallidiores. A *M. tuberculata* (O. F. Muller, 1774) testa graciliore, nodis majoribus et altitudine spire maiore distincta.

COI p-dist. 8.4% ab *M. tuberculata*.

Etymology: Named after the Khumbu region of Nepal in which the Arun River headwaters arise.

Preliminary IUCN: Endangered B1ab(iii); EOO = 340 km²; threats: upstream dam proposals; gravel extraction.

FAMILY PACHYCHILIDAE

Sulcospira meghnaensis Bianchi, Moreau & Silva, sp. nov.

Type material: Holotype NHML 2021.10.3.1; Paratypes: 22 shells + 10 tissues (NHML 2021.10.3.2-33; BARU-Z 2021-0848).

Type locality: Meghna River at Comilla, Comilla District, Bangladesh; 23.44N 91.18E; altitude 8 m; hard clay substrate in lower river reach.

Latin diagnosis: Testa elongata, fusiformis, altitudinis 35-47 mm; anfractus 10-11; costae spirales 8-10 per anfractu, robustae, confertae; color fusco-niger, nitidus; apertura ovato-angulata, canali brevi. A *S. testudinaria* (Mousson, 1849) testa majore, costis spiralibus crebrioribus et coloratione uniformiter fusco-nigra distincta. COI p-dist. 11.4% -- most divergent new species.

Etymology: Named after the Meghna River of Bangladesh.

Preliminary IUCN: Endangered B1ab(iii); EOO = 180 km²; threats: river dredging; industrial effluent.