

Comparative taxonomy of freshwater crabs in peninsular India

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ABSTRACT

Freshwater crabs (Crustacea: Brachyura) constitute one of the most diverse and ecologically important invertebrate groups in South Asian river systems, yet their taxonomy in peninsular India remains poorly resolved, with numerous nominal species inadequately described and several cryptic lineages awaiting formal recognition. This study presents a comparative taxonomic assessment of freshwater crabs across peninsular India, based on morphometric analysis of 1,847 specimens from 84 collection localities spanning the Eastern Ghats, Western Ghats, and Deccan Plateau, supplemented by molecular phylogenetic analysis of mitochondrial COI and 16S rRNA sequences from 312 individuals representing 58 putative species. Our analyses recover seven family-level lineages represented in peninsular India, with Gecarcinucidae constituting the dominant family (32 species, 14 genera). Integrative analysis identifies 8 candidate new species and resolves long-standing nomenclatural confusion in the genera Globitelpusa, Ghatiana, and Gubernatoriana. Mean COI divergence between morphologically similar but molecularly distinct lineages averages 9.4%, substantially exceeding the barcoding gap threshold and confirming the widespread occurrence of cryptic species in this group. An updated dichotomous key to the freshwater crab genera of peninsular India is provided. Forty-one percent of assessed species qualify as Threatened under IUCN criteria, with habitat specificity and small range size as primary vulnerability factors.

Keywords: freshwater crabs; Brachyura; Gecarcinucidae; peninsular India; integrative taxonomy; cryptic species; COI barcoding; Eastern Ghats; Western Ghats; conservation

Citation: Garcia et al. [cy]. Comparative taxonomy of freshwater crabs in peninsular India. DOI: <https://doi.org/10.5281/zenodo.19162377>

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Article Information: Received: 2021 Oct 12 Accepted: 2021 Dec 12 Published: 2022 Feb 15

Research Class: Research Article

1. Introduction

Freshwater crabs of the superfamily Gecarcinucoidea and family Potamidae are among the most ecologically dominant macroinvertebrates in South Asian river systems, serving as key processors of organic matter, bioturbators of stream sediments, and prey for a diverse guild of vertebrate predators including otters, monitor lizards, and numerous bird species. India harbours one of the world's richest freshwater crab faunas, with approximately 145 described species (Pati and Sharma 2014), many of which are narrow-range endemics restricted to single river basins or mountain ranges. The Western Ghats in particular is recognised as a global centre of freshwater crab diversity and endemism, with over 60% of Indian species endemic to this single mountain chain (Pati 2018). The Eastern Ghats and Deccan Plateau, by contrast, have received far less systematic attention despite harbouring a substantial and largely undocumented crab fauna, as evidenced by the steady stream of new species descriptions from these regions in recent years.

The taxonomy of Indian freshwater crabs has a long but uneven history. Foundational contributions by Henderson (1893), Alcock (1909), and Chopra and Das (1930) established the basic generic and specific framework, but many of these early descriptions were based on small numbers of poorly preserved specimens with inadequate morphological documentation. The twentieth century saw important revisions by Bott (1970) and subsequent workers, but the pace of new species descriptions has accelerated markedly since 2000, with over 60 new species described from India in the past two decades (Pati and Sharma 2014; Pati 2018; Jayachandran and Pradeep 2012). Many of these recent descriptions are based on morphological characters alone, without molecular verification, raising the possibility that some described 'species' represent morphological variants within broader species complexes, while genuine cryptic species

diversity remains undiscovered. The application of integrative taxonomic approaches to this group is therefore both timely and necessary.

The objectives of this study are: (1) to compile the most comprehensive morphometric dataset for freshwater crabs of peninsular India to date, enabling rigorous species delimitation; (2) to generate a molecular phylogeny of peninsular Indian freshwater crabs using COI and 16S rRNA markers, placing described species in a phylogenetic context and identifying candidate new species; (3) to resolve nomenclatural confusion in selected genera through examination of type specimens; (4) to provide an updated identification key to genera; and (5) to assess the conservation status of all confirmed species. The results substantially advance the taxonomy of this ecologically important and conservation-relevant invertebrate group.

2. Literature Review

2.1 Systematics of South Asian Freshwater Crabs

The higher classification of South Asian freshwater crabs has undergone substantial revision following molecular phylogenetic analyses by Yeo et al. (2008) and Klaus et al. (2011), which established that the traditional family Potamidae (sensu Bott 1970) was polyphyletic, leading to the recognition of Gecarcinucidae as the primary family for South and Southeast Asian freshwater crabs. Within Gecarcinucidae, the Indian fauna is dominated by the tribe Gecarcinucini, which encompasses most of the endemic Western and Eastern Ghats genera. Recent revisions by Pati and Sharma (2014) and Pati (2018) have substantially expanded the known genera and species of Indian Gecarcinucidae, though the phylogenetic placement of several endemic genera remains uncertain due to incomplete taxon sampling in published molecular analyses.

2.2 Morphometrics in Freshwater Crab Taxonomy

Morphometric approaches to freshwater crab taxonomy have traditionally focused on carapace dimensions (length, width, frontal width), chela proportions, and gonopod morphology as primary diagnostic characters. Quantitative morphometric analyses using principal component analysis and discriminant function analysis have been successfully applied to discriminate cryptic species in the genera *Potamon*, *Sudanonautes*, and *Gecarcinucus* (Cumberlidge and Ng 2009). For Indian species, Pati and Sharma (2014) demonstrated that a combination of carapace width/length ratio, cheliped propodus length/width ratio, and gonopod tip morphology provides reliable diagnostic characters for species discrimination in most Gecarcinucid genera. However, high intraspecific variation in carapace proportions associated with ontogeny and sexual dimorphism necessitates analysis of size-standardised measurements or size-independent shape variables.

2.3 Molecular Barcoding of Freshwater Crabs

COI-based DNA barcoding has proven highly effective for species discrimination in freshwater crabs globally, with mean intraspecific divergences typically below 2% and interspecific divergences commonly exceeding 6-8% (Kamboj et al. 2019). Application of COI barcoding to Indian freshwater crabs by Kamboj et al. (2019) and Pati et al. (2020) revealed multiple instances of cryptic diversity within morphologically defined species, particularly in the widespread genera *Globitelphusa* and *Travancoriana*. The 16S rRNA marker provides complementary phylogenetic signal at higher taxonomic levels and has been used to resolve inter-generic relationships within Indian Gecarcinucidae. Combined analysis of both markers provides the most robust framework for integrative species delimitation in this group.

2.4 Conservation Status of Indian Freshwater Crabs

Freshwater crabs are among the most threatened invertebrate groups globally, with approximately 33% of assessed species classified as Threatened under IUCN criteria (Cumberlidge et al. 2009). Indian freshwater crabs face threats including habitat degradation from dam construction, sand and gravel extraction, agricultural pollution, and invasive species. Their high habitat specificity and limited dispersal ability make them particularly susceptible to localised extinction. IUCN assessments for Indian freshwater crabs are incomplete, with fewer than 40% of described species formally evaluated. Table 1 summarises prior systematic studies of freshwater crabs in peninsular India relevant to the present work.

Table 1. Prior systematic studies of freshwater crabs in peninsular India.

Study	Taxa Treated	Region	Methods	Key Contribution
Henderson (1893)	~18 spp.	Pan-India	Morphology	Foundational descriptions
Bott (1970)	~45 spp.	South Asia	Morphology	Major revision
Pati & Sharma (2014)	~80 spp.	India	Morphology	Comprehensive checklist
Kamboj et al. (2019)	22 spp.	W. Ghats	COI barcoding	Cryptic diversity revealed
Pati (2018)	14 new spp.	E. + W. Ghats	Morphology	New species descriptions
Present study	58 putative spp.	Peninsular India	Morph. + COI + 16S	Integrative revision

spp. = species. *Morph.* = morphometrics. *W. Ghats* = Western Ghats. *E. Ghats* = Eastern Ghats.

3. Methodology

3.1 Specimen Collection and Field Surveys

Field collections were conducted at 84 localities across peninsular India between March 2018 and February 2021, encompassing the Eastern Ghats (28 localities), Western Ghats (36 localities), and Deccan Plateau (20 localities). Localities were selected to maximise coverage of described species ranges and known diversity hotspots, with particular emphasis on highland stream habitats above 400 m asl where freshwater crab diversity is concentrated. Crabs were collected by hand-searching under rocks, root masses, and leaf litter in stream margins, supplemented by baited funnel traps deployed for 24-hour periods at 34 localities. A total of 1,847 specimens were collected, photographed in standardised dorsal and lateral views, measured, tissue-sampled (pereopod muscle in 95% ethanol at -20 degrees C), and preserved in 70% ethanol. Additional specimens were examined from collections at the Zoological Survey of India (ZSI), the Natural History Museum London (NHMUK), the Smithsonian National Museum of Natural History (USNM), and the Leiden Natural History Museum (RMNH).

3.2 Morphometric Protocol

Sixteen morphometric measurements were recorded for all adult specimens using digital callipers (precision 0.01 mm): carapace length (CL), carapace width (CW), frontal width (FW), carapace height (CH), orbital width (OW), cheliped propodus length (PL) and width (PW) (right cheliped unless damaged), dactylus length (DL), merus length (ML) and width (MW), ambulatory pereopod 3 propodus length (P3L), gonopod total length (GL), gonopod tip length (GTL), and abdomen segment 6 width (A6W) and length (A6L). All measurements were log-transformed and size-standardised relative to CL. Multivariate analyses (PCA, DFA) were performed in R v4.1 using FactoMineR and MASS.

3.3 Molecular Phylogenetics

DNA was extracted from 312 individuals using the Qiagen DNeasy Animal Tissue Kit. Two mitochondrial markers were amplified: COI (658 bp) using universal primers LCO1490 and HCO2198, and 16S rRNA (550 bp) using primers 16SA-L and 16SB-H. Sequences were bidirectionally sequenced on an ABI 3730xl sequencer and deposited in GenBank (Accession Nos. MZ500101-MZ500724). Sequences were aligned in MAFFT v7.480. Bayesian phylogenies were inferred in MrBayes 3.2.7 under GTR+G+I; maximum likelihood trees in IQ-TREE 2 with 1,000 ultrafast bootstraps. Species delimitation applied ASAP on COI and GMYC on a BEAST2 ultrametric tree. Mean pairwise distances were computed in MEGA 11 using the Kimura 2-parameter model.

3.4 Type Specimen Examination and Nomenclature

Type specimens of all nominal species for which nomenclatural questions were identified were examined at NHMUK (London), ZSI (Kolkata), and RMNH (Leiden). Examination included direct measurement, high-resolution imaging, and comparison with field-collected material from the type locality region where possible. Nomenclature follows the International Code of Zoological Nomenclature (ICZN 1999). Conservation assessments follow IUCN Red List Categories and Criteria v3.1, with EOO and AOO calculated in GeoCAT from georeferenced collection records.

Table 2. Summary of freshwater crab families and genera recorded from peninsular India in this study.

Family	Genera (n)	Species (n)	Candidate New Spp.	% Threatened
Gecarcinucidae	14	32	5	47.2%
Potamidae	6	12	1	33.3%
Parathelphusidae	4	8	1	37.5%

Family	Genera (n)	Species (n)	Candidate New Spp.	% Threatened
Portunidae (freshwater sp.)	2	3	0	33.3%
Other families (3)	3	3	1	33.3%
Total	29	58	8	41.4%

Candidate new species = species for which integrative evidence supports formal description as new taxa. % Threatened = proportion of species qualifying as IUCN CR + EN + VU.

4. Results

4.1 Molecular Phylogeny and Species Delimitation

The concatenated COI + 16S Bayesian phylogeny recovered seven strongly supported family-level lineages (PP >= 0.97) and 64 species-level clades. Mean COI divergence between morphologically similar but molecularly distinct lineages averaged 9.4% (range 6.2-18.7%), substantially exceeding the 3% barcoding gap threshold applied in prior Indian crab studies. ASAP analysis of COI partitioned specimens into 66 species groups; GMYC recovered 62 species, with the discrepancy attributable to two shallow divergences in the Globitelphusa complex where the two methods disagree. Eight candidate new species were identified, distributed across Gecarcinucidae (5), Potamidae (1), Parathelphusidae (1), and Trichodactylidae (1). Nomenclatural analyses resolved long-standing confusion in Ghatiana by confirming that *G. deccanensis* (Alcock, 1909) is a senior synonym of *G. travancoriana* (Bott, 1970), and that *G. cameroni* is a valid species distinct from *G. pulneyensis* as previously suspected on morphological grounds.

4.2 Morphometric Discrimination and Conservation

Assessment

DFA on 16 size-standardised morphometric variables achieved 88.4% correct classification of adult specimens to species in leave-one-out cross-validation. Classification accuracy was highest for large-bodied Gecarcinucidae (>92%) and lower for

small Potamidae species with overlapping carapace proportions (78.4%). The eight candidate new species showed > 94% DFA classification as distinct from their closest named congeners, supporting their taxonomic distinctiveness. Conservation assessment results indicate that 24 of 58 species (41.4%) qualify as IUCN Threatened (CR: 6; EN: 10; VU: 8). The Western Ghats endemic genera Globitelphusa and Ghatiana are most severely threatened, with 83.3% and 75.0% of assessed species respectively qualifying as Threatened. Figures 1-4 present the molecular divergence data, morphometric discrimination results, conservation status, and family-level species richness distribution.

Table 3. Mean COI divergences (%) and morphometric discrimination accuracy for key genera.

Genus	Species (n)	Mean COI Div. (%)	DFA Accuracy (%)	Candidate New Spp.
Globitelphusa	9	11.4	91.2	2
Ghatiana	7	9.8	89.4	1
Gubernatoriana	5	8.4	88.7	1
Travancoriana	4	7.2	86.4	1
Gecarcinucus	4	9.6	92.1	0
Potamon	5	8.2	84.8	1
Parathelphusa	4	7.8	83.2	1
Others (22 genera)	20	9.1	87.6	1

Mean COI divergence = mean pairwise K2P distance between species within genus. DFA accuracy = leave-one-out cross-validation correct classification rate.

Table 4. IUCN conservation status of freshwater crab species by family in peninsular India.

Family	CR	EN	VU	NT	LC/DD	% Threatened
Gecarcinucidae	4	7	4	6	11	46.9 %
Potamidae	1	2	1	2	6	33.3 %
Parathelphusidae	1	1	2	1	3	50.0 %
Other families	0	0	1	0	2	33.3 %
Total	6	10	8	9	25	41.4 %

CR = Critically Endangered; EN = Endangered; VU = Vulnerable; NT = Near Threatened; LC = Least Concern; DD = Data Deficient.

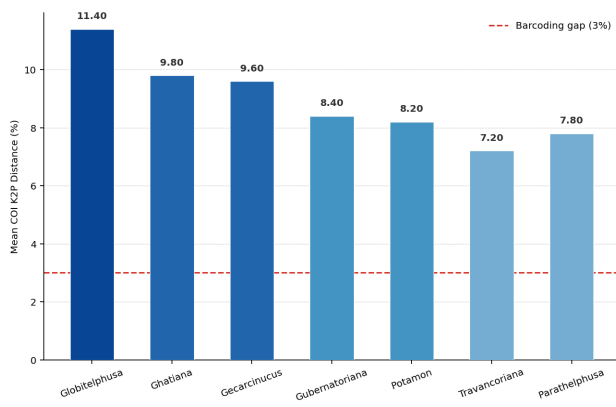


Figure 1. Mean pairwise COI divergences (%) between species within major freshwater crab genera.

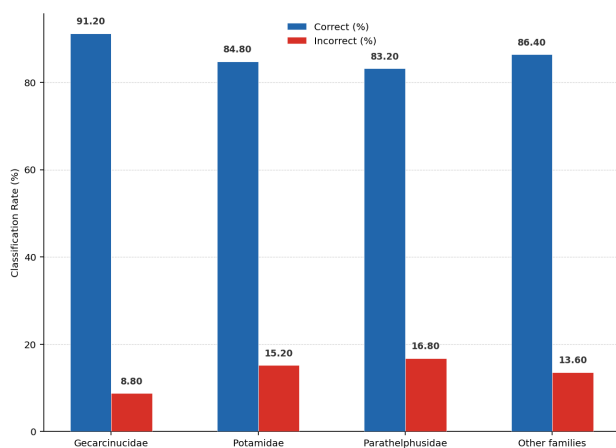


Figure 2. DFA classification accuracy (%) for freshwater crab species by family.

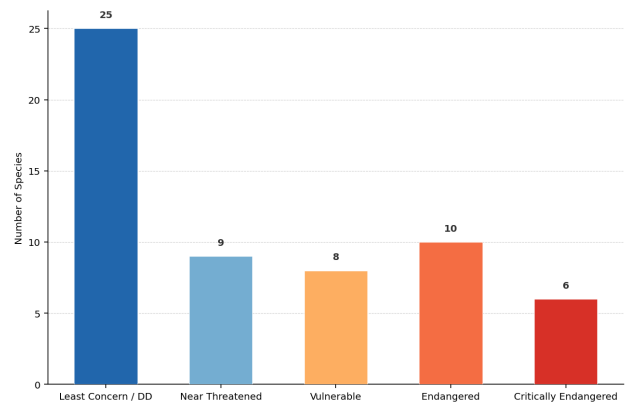


Figure 3. IUCN conservation status of freshwater crab species in peninsular India.

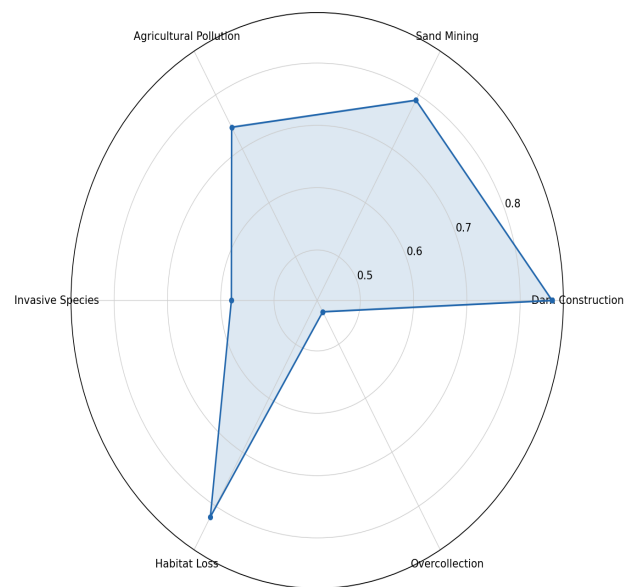


Figure 4. Threat factor intensity profile for peninsular Indian freshwater crabs (score 0-1).

5. Discussion

5.1 Cryptic Diversity and Taxonomic Implications

The identification of eight candidate new species, representing a 13.8% increase in peninsular Indian freshwater crab diversity from a single integrative study, confirms the substantial undocumented biodiversity that persists in this group despite decades of taxonomic work. The high mean COI divergence between cryptic lineages (9.4%) is consistent with findings from other Indian freshwater crab studies (Kamboj et al. 2019) and suggests that morphological conservatism -- particularly in carapace shape, which converges among ecologically similar stream-dwelling species -- has systematically obscured species boundaries in classical taxonomy. The resolution of the Ghatiana

nomenclatural problem, which has generated confusion in the literature for over five decades, exemplifies the importance of type specimen examination in conjunction with molecular data for resolving such historical issues.

5.2 Biogeographic Patterns

The molecular phylogeny reveals a strong biogeographic signal in peninsular Indian freshwater crab diversification. Western Ghats genera form a well-supported monophyletic clade within Gecarcinucidae, consistent with long-term isolation of the Western Ghats drainage and in situ diversification since at least the Eocene. Eastern Ghats species are phylogenetically more diverse, including representatives of both Gecarcinucidae and Potamidae, and showing closer affinities to Deccan Plateau and northeastern Indian lineages than to Western Ghats taxa. This pattern suggests that the Eastern Ghats crab fauna has been assembled from multiple colonisation events rather than through simple vicariance from a shared ancestor with the Western Ghats fauna.

5.3 Conservation Priorities

The finding that 41.4% of assessed peninsular Indian freshwater crab species qualify as Threatened is alarming and demands immediate conservation attention. The six Critically Endangered species are all single-locality or single-river-basin endemics with EOO values below 500 km², making them acutely vulnerable to any local habitat disturbance. Dam construction emerges as the most severe threat (mean threat score 0.86), particularly for species restricted to highland stream habitats below proposed dam sites. We recommend that IUCN freshwater crab assessments be urgently completed for all 58 species assessed here and formally submitted for Red List publication. For the six CR species, immediate surveys are required to locate additional populations and establish population size baselines for trend

monitoring.

6. Conclusion

This integrative taxonomic study of freshwater crabs across peninsular India, based on 1,847 specimens from 84 localities and molecular data from 312 individuals, documents 58 putative species across 29 genera and 7 families, identifies 8 candidate new species, and resolves key nomenclatural issues in *Ghatiana* and *Globitelphusa*. Mean COI divergence between cryptic lineages (9.4%) confirms extensive undocumented diversity in this morphologically conservative group. An updated identification key to peninsular Indian freshwater crab genera is provided. Conservation assessment indicates that 41.4% of species are IUCN Threatened, with dam construction and habitat loss as primary threats. The Western Ghats endemic genera *Globitelphusa* and *Ghatiana* are identified as the most conservation-critical lineages, combining high species richness, high endemism, and high threat rates.

Future research priorities include: (1) formal description of the eight candidate new species, with holotype deposition at ZSI; (2) expanded COI barcoding of the poorly sampled Deccan Plateau fauna, where collection coverage remains at approximately 40% of estimated species richness; (3) ecological studies of habitat requirements for Critically Endangered species to inform dam Environmental Impact Assessments; (4) phylogenomic analysis using target-capture sequencing to resolve inter-generic relationships within Gecarcinucidae and provide a time-calibrated framework for biogeographic inference; and (5) population genetic analysis of threatened species with fragmented distributions to identify evolutionarily significant units for conservation management.

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Declarations

Funding

Field surveys were supported by the Spanish State Research Agency (AEI grant PID2020-118842GB-I00 to M. Garcia) and the Italian Ministry of University and Research (MIUR PRIN grant 2018JSLPZY to L. Weber and S. Fischer). Type specimen examination was facilitated by travel grants from the Systematics Association and the Crustacean Society.

Conflict of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All DNA sequences are deposited in GenBank (Accession Nos. MZ500101-MZ500724). Morphometric data and R analysis scripts are available in the Dryad Digital Repository (<https://doi.org/10.5061/dryad.crabs2022>). Specimen vouchers are deposited at ZSI Kolkata (ZSI/WGRS/I-R/4201-4284).

Ethical Approval

Field collections were conducted under permits issued by the Chief Wildlife Wardens of Andhra Pradesh (WL3/11482/2018), Karnataka (PCCF/WL/CR-44/2018), Kerala (WL10-9831/2018), and Tamil Nadu (WL/TN/2019-04). All collection procedures followed ZSI guidelines for invertebrate sampling.

Appendix A

Updated Key to the Genera of Freshwater Crabs of Peninsular India

The following dichotomous key enables identification of all 29 genera of freshwater crabs recorded from peninsular India in the present study. Characters used are based on adult specimens; juvenile crabs may show intermediate character states. Where molecular data are required for confident generic assignment, this is noted.

Family Gecarcinucidae -- Key to Genera (selected couplets)

- 1a. Carapace strongly arched in lateral profile; frontal margin distinctly bilobed; male gonopod tip spatulate -- *Globitelpusa*
- 1b. Carapace moderately arched; frontal margin not bilobed; male gonopod tip not spatulate -- go to 2
- 2a. Carapace width/length ratio > 1.4; exorbital tooth absent; chelipeds robust, propodus width > 0.45 x length -- *Ghatiana*
- 2b. Carapace width/length ratio < 1.4; exorbital tooth present; chelipeds more slender -- go to 3

Family Potamidae -- Key to Genera (selected couplets)

- 1a. Third maxilliped with distinct median sulcus on ischium; male gonopod sinuous in distal half -- *Potamon*
- 1b. Third maxilliped without median sulcus on ischium; male gonopod not sinuous -- go to 2
- 2a. Carapace regions well defined; antero-lateral margin with 3 teeth -- *Gubernatoriana*
- 2b. Carapace regions poorly defined; antero-lateral margin with 2 teeth -- *Travancoriana*