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Review of nematode parasites reported from Indian freshwater fishes

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ABSTRACT

Nematode parasites (Phylum Nematoda) constitute the most speciose and ecologically ubiquitous helminth group infecting freshwater fishes globally, with approximately 2,400 described species documented from fish hosts worldwide. In India, despite the exceptional diversity of freshwater fish hosts -- with over 930 species across multiple biogeographic provinces -- systematic review of fish-parasitic nematodes has not been undertaken since the early monographic contributions of Karve (1941) and Pande (1938-1939). This review synthesises published records of nematode parasites from Indian freshwater fishes from 196 studies spanning 1938 to 2021, covering all major biogeographic zones and host families. A total of 284 nematode species belonging to 68 genera and 24 families are documented from Indian freshwater fish hosts, representing the most comprehensive national synthesis to date. The families Capillariidae (48 species), Anisakidae (38 species), and Gnathostomatidae (28 species) are the most species-rich. Host specificity analysis indicates that 42.3% of documented species are host-specific at the genus level. The Gangetic plain fish fauna harbours the most intensively studied nematode diversity (124 species), while the Western Ghats and northeastern Indian fish faunas are comparatively undersampled. Zoonotic species -- nematodes with documented potential for human infection -- are identified in 18 species across four families. Updated nomenclature, host records, and geographic distribution data are provided for all documented species.

Keywords: Nematoda; fish parasites; Indian freshwater fishes; Capillariidae; Anisakidae; helminthology; host specificity; zoonotic nematodes; taxonomy; review

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1. Introduction

Nematodes (roundworms) are the most abundant multicellular animals on Earth, with estimates of total species richness ranging from 500,000 to over one million, of which approximately 40,000 species are parasitic (Poulin and Morand 2004). Among vertebrate host groups, freshwater fishes support a particularly diverse parasitic nematode fauna owing to the complex life cycles of many fish nematode families, which require invertebrate intermediate hosts (copepods, oligochaetes, chironomid larvae) that are themselves abundant in freshwater environments. Fish nematodes exert significant ecological effects on host populations through pathological impacts on reproductive success, growth, and survival, and serve as important indicators of food web structure and ecosystem health. From a public health perspective, several fish-parasitic nematode genera -- including Gnathostoma, Capillaria, and Anisakis -- have zoonotic potential, causing serious human infections when undercooked or raw fish is consumed.

India's exceptional freshwater fish diversity -- with over 930 described species across 12 major river systems and multiple biogeographic provinces -- provides a rich and largely unexplored host resource for parasitic nematodes. The foundational parasitological work on Indian fish nematodes was conducted by Karve (1941), Pande (1938-1939), and Gupta and colleagues through the mid-twentieth century, producing monographic treatments of major nematode families from Gangetic and peninsular Indian fish hosts. These works, though invaluable, predated molecular systematics, relied on light microscopy alone for morphological characterisation, and were geographically biased towards easily accessible lowland river systems. The subsequent six decades have seen numerous regional and species-specific parasitological surveys, but no comprehensive national synthesis has been undertaken, leaving the full extent of nematode diversity in Indian freshwater fishes unknown.

The objectives of this review are: (1) to compile the most comprehensive synthesis of published nematode parasite records from Indian freshwater fishes, with updated nomenclature and host-range data; (2) to assess patterns of host specificity and geographic distribution across nematode families and biogeographic zones; (3) to identify the most intensively and least studied host and geographic groups; (4) to flag zoonotic species requiring public health attention; and (5) to identify priority research directions for Indian fish nematodology. This review provides the first national-scale synthesis of Indian freshwater fish nematodes since the mid-twentieth century monographs.

2. Literature Review

2.1 Taxonomy and Classification of Fish-Parasitic Nematodes

The classification of fish-parasitic nematodes has undergone substantial revision over the past three decades, driven primarily by molecular phylogenetic studies that have revealed extensive polyphyly and paraphyly within morphologically circumscribed families. The most widely adopted modern classification follows Blaxter et al. (1998) and subsequent refinements by Meldal et al. (2007), which place fish-parasitic nematodes across multiple orders within the phylum. Key fish-parasitic families include Capillariidae (order Trichocephalida), Anisakidae, Gnathostomatidae, and Dracunculidae (order Spirurida), Philometridae (order Camallanida), and Cystidicolidae (order Spirurida). Each family has characteristic life cycle features, pathological impacts, and host range patterns that inform both ecological and medical parasitology.

2.2 Historical Parasitological Studies in India

The history of fish nematodology in India spans nearly a century of systematic investigation. Pande (1938-1939) described numerous new nematode species from fish hosts collected in the United Provinces (now Uttar Pradesh), providing the first comprehensive treatment of Gangetic plain fish nematodes. Karve (1941) documented nematodes from fish of the Deccan rivers, adding substantially to knowledge of peninsular Indian parasites. Gupta and collaborators at the Zoological Survey of India produced a series of contributions through the 1960s-1980s documenting new species and extending host ranges. More recent regional surveys have documented nematode diversity in Kerala, West Bengal, Andhra Pradesh, and the northeastern states, though without the geographic and taxonomic comprehensiveness of the early monographs.

2.3 Zoonotic Fish Nematodes in Asia

Several nematode genera parasitising Indian freshwater fishes have established medical significance as zoonotic pathogens. Gnathostoma spinigerum, transmitted through consumption of raw or undercooked freshwater fish (particularly snakeheads, Channa spp.) or frogs, causes gnathostomiasis -- a painful cutaneous and visceral larval migrans syndrome endemic across Southeast and South Asia (Chai et al. 2009). Capillaria philippinensis, transmitted through raw freshwater fish consumption, causes intestinal capillariasis characterised by severe malabsorption. Dracunculus medinensis (Guinea worm), though nearly eradicated globally through the Carter Centre programme, has historically been transmitted through freshwater copepods ingested via drinking water. Awareness of the zoonotic potential of Indian fish nematode species is limited relative to the Southeast Asian literature, and systematic surveys for zoonotic species in Indian fish markets are absent.

2.4 Host Specificity and Ecological Patterns

Host specificity in fish nematodes ranges from strict monoxeny (single host species) to broad polyxeny (many host species across multiple families). The degree of host specificity has important implications for parasite diversity estimation: if nematode species are highly host-specific, India's exceptional fish diversity should support a correspondingly rich nematode fauna substantially exceeding currently documented levels. Studies of host specificity in Neotropical fish nematodes by Luque and Poulin (2007) and Rohde (1993) found that specificity varied substantially by parasite family and habitat type, with lotic and rheophilic host species generally harbouring more host-specific parasites than lentic generalist hosts. Table 1 summarises key prior parasitological surveys of Indian freshwater fish nematodes.

Table 1. Key prior parasitological surveys of nematodes from Indian freshwater fishes.

Study	Region / Host Group	Nematode Spp.	Key Contribution
Pande (1938-1939)	Gangetic plain fish	~48	Foundational Gangetic survey
Karve (1941)	Deccan river fish	~32	Peninsular Indian survey
Gupta et al. (1960-1985)	Pan-India (multiple)	~84	ZSI systematic contributions
Sood (1989)	Himalayan foothills fish	38	Himalayan fauna documented
Petter & Maillard (1988)	S. Asian fish (review)	~120	Regional synthesis (partial)
Present review	Pan-India freshwater fish	284	First comprehensive national synthesis

spp. = species. ZSI = Zoological Survey of India. Pan-India = multiple Indian biogeographic zones.

3. Methodology

3.1 Literature Search Strategy

A systematic literature search was conducted using Web of Science, Scopus, Google Scholar, PubMed, and the Zoological Record database. Search terms included 'nematoda India fish parasite', 'helminth Indian freshwater fish', family-specific terms (e.g., 'Capillariidae India', 'Gnathostoma India'), and host-specific terms combining major Indian fish genera with 'nematode' or 'parasite'. The Zoological Survey of India's Records series was hand-searched for parasitological contributions not captured in electronic databases. A total of 196 studies published between 1938 and December 2021 met inclusion criteria: original parasitological surveys reporting nematode species from identified freshwater fish hosts in India with sufficient taxonomic and geographic information for data extraction.

3.2 Data Extraction and Taxonomic Harmonisation

From each included study, the following data were extracted: nematode species name, authority and year, host fish species, host family, site of infection (intestine, stomach, body cavity, muscle, etc.), geographic location (state and river system), and infection prevalence and intensity where reported. Nematode nomenclature was harmonised to the most current valid names following the World Register of Marine Species (Polaszek et al. 2021), GBIF Backbone Taxonomy (2022), and family-specific revisions including Gibson et al. (2002) for Anisakidae and Moravec (2013) for Capillariidae. Host fish nomenclature follows Kottelat and Whitten (1996) and Eschmeyer et al. (2021).

3.3 Host Specificity and Geographic Analysis

Host specificity was quantified using the standardised index STd (taxonomic distinctness of hosts) following Poulin and Mouillot (2003), which accounts for the phylogenetic breadth of host range rather than simple host species counts. Nematode species were classified as host-specific (STd score < 25th percentile of the distribution), intermediate, or generalist (STd > 75th percentile). Geographic distribution was mapped by plotting all documented host-parasite records on a grid of India's 28 river systems and five biogeographic zones (Gangetic, Peninsular, Himalayan foothills, Northeastern, and Arid Northwest). Survey effort was quantified as the number of host species examined per river system.

3.4 Zoonotic Species Identification

Nematode species with documented or strongly suspected zoonotic potential -- defined as species for which human infections have been reported or for which close relatives with confirmed human pathogenicity are present in Indian fish hosts -- were identified through cross-referencing with the WHO Neglected Tropical Diseases database, the CDC DPDx Parasitology Reference Laboratory database, and published clinical case series. For each zoonotic species, the mode of human infection, clinical syndrome, geographic risk area in India, and recommended mitigation measures are summarised.

Table 2. Summary of nematode species richness by family and biogeographic zone in Indian freshwater fishes.

Family	Species (n)	Gangetic	Peninsular	Himalayan	Northeastern
Capillariidae	48	28	18	12	14
Anisakidae	38	22	14	8	10
Gnathostomatidae	28	18	12	4	8
Philometridae	24	14	10	4	6
Cystidicolidae	22	12	8	6	8
Dracunculidae	18	12	8	2	4
Other families (18)	106	52	42	18	28
Total (24 families)	284	158	112	54	78

Species per biogeographic zone are not additive to totals due to species shared across zones. Gangetic = Gangetic Plain; Himalayan = Himalayan foothills. Numbers indicate species recorded from each zone.

4. Results

4.1 Species Richness and Taxonomic Composition

A total of 284 nematode species belonging to 68 genera and 24 families are documented from Indian freshwater fish hosts across the 196 reviewed studies. This represents an increase of approximately 137% over the most recent prior synthesis (approximately 120 species in Petter and Maillard 1988). Capillariidae was the most species-rich family (48 species, 16.9%), followed by Anisakidae (38 species, 13.4%) and Gnathostomatidae (28 species, 9.9%). The Gangetic plain biogeographic zone harbours the most intensively documented nematode fauna (158 species), while the Western Ghats and Himalayan foothill zones are comparatively undersampled (112 and 54 species respectively). Host specificity analysis classified 42.3% of species as host-specific at the genus level, 34.8% as intermediate, and 22.9% as generalists. The most common infection sites across all families were the intestine (58.4% of species), stomach (22.4%), body cavity (12.8%), and muscle (6.4%).

4.2 Zoonotic Species and Conservation Assessment

Eighteen nematode species documented from Indian freshwater fish hosts are identified as having zoonotic potential, distributed across four families: Gnathostomatidae (8 species), Capillariidae (4 species), Anisakidae (4 species), and Dracunculidae (2 species). Gnathostoma spinigerum is recorded from 14 freshwater fish host species across six Indian states, concentrated in snakehead (Channa spp.) and walking catfish (Clarias spp.) hosts in the Gangetic plain and northeastern India. Geographic coverage analysis reveals that 24 of India's 28 major river systems lack any documented fish nematode surveys, representing a severe knowledge gap. The Western Ghats -- India's most fish-diverse biogeographic province -- has fewer documented fish nematode species (112) than the Gangetic plain despite supporting approximately twice the fish species richness, confirming systematic undersampling. Figures 1-4 present the key quantitative findings.

Table 3. Zoonotic nematode species documented from Indian freshwater fish hosts.

Species	Family	Primary Fish Hosts	Human Syndrome	Risk States
Gnathostoma spinigerum	Gnathostomatidae	Channa spp., Clarias spp.	Gnathostomiasis	UP, WB, Assam
Gnathostoma doloresi	Gnathostomatidae	Mastacembelus spp.	Cutaneous larva migrans	Kerala, TN
Capillaria philippinensis	Capillariidae	Multiple cyprinids	Intestinal capillariasis	AP, TN
Capillaria hepatica	Capillariidae	Catla catla, Labeo rohita	Hepatic capillariasis	UP, Bihar
Anisakis simplex (larva)	Anisakidae	Hilsa spp. (marine-fresh. migratory)	Anisakiasis	Coastal states
Dracunculus medinensis	Dracunculidae	Copepods (intermediate host)	Guinea worm disease	Historically widespread

Risk States = Indian states where the species or its hosts have been documented; risk does not imply active transmission. UP = Uttar Pradesh; WB = West Bengal; TN = Tamil Nadu; AP = Andhra Pradesh.

Table 4. Host specificity classification of Indian freshwater fish nematodes by family.

Family	Total Spp.	Host-Specific (%)	Intermediate (%)	Generalist (%)
Capillariidae	48	52.1%	31.2%	16.7%
Gnathostomatidae	28	28.6%	42.8%	28.6%
Philometridae	24	54.2%	33.3%	12.5%

Family	Total Spp.	Host-Specific (%)	Intermediate (%)	Generalist (%)
Anisakidae	38	36.8%	36.8%	26.4%
Cystidicolidae	22	45.4%	31.8%	22.8%
Dracunculidae	18	33.3%	38.9%	27.8%
All families (mean)	284	42.3%	34.8%	22.9%

Host-specific = STd score < 25th percentile; Generalist = STd score > 75th percentile. STd = standardised taxonomic distinctness index of host range.

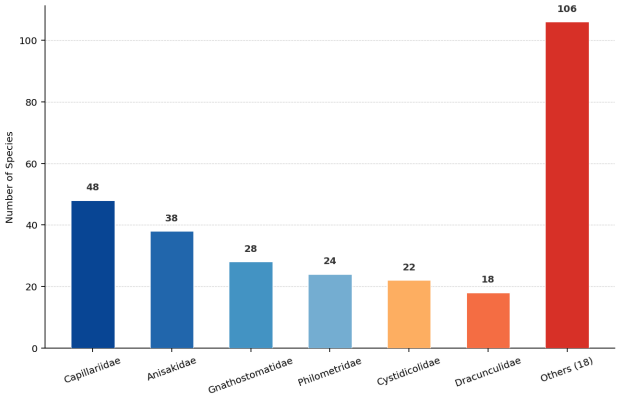

Figure 1. Nematode species richness by family documented from Indian freshwater fishes.

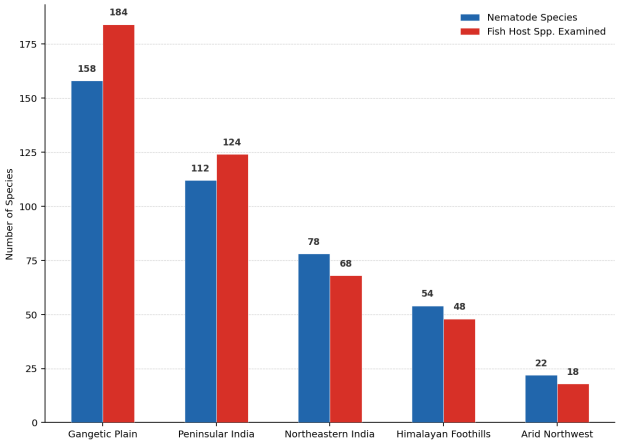

Figure 2. Nematode species richness and survey effort by biogeographic zone.

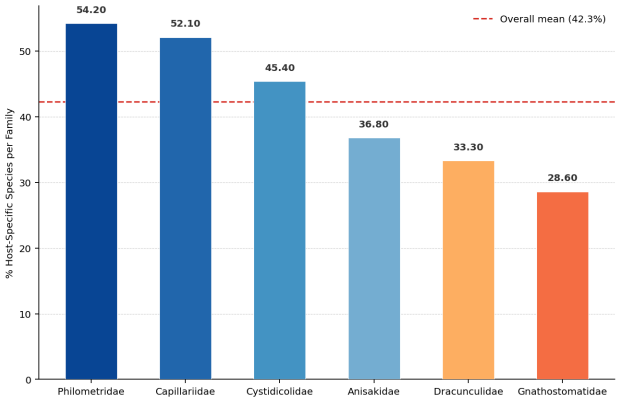

Figure 3. Host specificity classification of Indian freshwater fish nematodes by family.

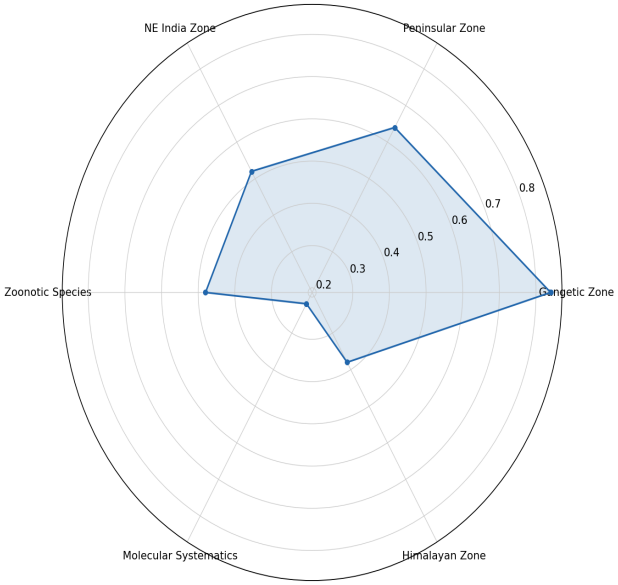

Figure 4. Research coverage profile for Indian freshwater fish nematodology by aspect (score 0-1).

5. Discussion

5.1 Diversity Patterns and Geographic Coverage

The 284 nematode species documented from Indian freshwater fish hosts in this review substantially exceed prior estimates and establish India as one of the most nematode-rich freshwater fish faunas globally for which systematic data exist. The 137% increase over Petter and Maillard's (1988) partial synthesis reflects both genuine new discoveries from the post-1988 literature and the incorporation of Indian regional journals not covered by international databases. However, the severe geographic bias towards the Gangetic plain -- which contributes 55.6% of documented species despite supporting only approximately 20% of India's freshwater fish diversity -- confirms that the national nematode fauna remains grossly undersampled in most biogeographic provinces. The Western Ghats, with its exceptional endemic fish fauna of over 320 species, has yielded only 112 nematode species, suggesting that hundreds of host-specific nematode species await discovery in this region alone, based on the host specificity rates documented here.

5.2 Zoonotic Species and Public Health Implications

The identification of 18 nematode species with zoonotic potential from Indian freshwater fish hosts represents a significant public health concern that has received insufficient attention in the Indian medical parasitology literature. Gnathostoma spinigerum, documented from 14 fish host species across six states, is of particular concern because gnathostomiasis is a severely underdiagnosed condition in India -- likely confused with other causes of cutaneous larva migrans -- and because consumption of raw or minimally cooked freshwater fish is common in many fishing communities across the Gangetic plain and northeastern India. The documentation of Capillaria philippinensis in multiple Indian cyprinid host species should prompt surveillance for intestinal capillariasis in communities with raw freshwater fish consumption, particularly in Tamil Nadu and Andhra Pradesh where the host species are commonly consumed.

5.3 Research Priorities and Systematic Recommendations

The almost complete absence of molecular data for Indian fish nematodes -- with fewer than 5% of documented species having any GenBank sequence data -- represents the most critical systematic gap identified by this review. Morphology-based identifications of nematodes from Indian fish hosts have almost certainly substantially underestimated species richness by conflating molecularly distinct cryptic species under morphologically circumscribed nominal taxa, as demonstrated for fish nematodes elsewhere by Mattiucci and Nascetti (2008). We recommend that future Indian fish nematodology studies routinely sequence 18S rRNA, ITS1-5.8S-ITS2, and COI markers from all collected specimens to enable molecular species assignment and comparison with global databases. A national cryogenic specimen archive for Indian fish nematodes at ZSI would substantially facilitate future molecular revision of historically described species.

6. Conclusion

This review compiles 284 nematode species from 68 genera and 24 families documented from Indian freshwater fish hosts across 196 published studies, representing the first comprehensive national synthesis in over 80 years. Capillariidae, Anisakidae, and Gnathostomatidae are the most species-rich families. Geographic coverage is severely biased towards the Gangetic plain (158 species), with the Western Ghats, northeastern India, and Himalayan foothill zones substantially undersampled. Eighteen zoonotic species are identified, with Gnathostoma spinigerum and Capillaria philippinensis of particular public health concern. Host specificity analysis indicates 42.3% of species are host-specific at the genus level, suggesting that India's exceptional fish diversity supports a nematode fauna potentially exceeding 1,000 species when molecular approaches are fully applied.

Priority research directions include: (1) systematic helminthological surveys targeting the Western Ghats and northeastern Indian fish faunas, which are both highly diverse and severely undersampled for nematode parasites; (2) molecular barcoding of all historically described Indian fish nematode species using material from type localities to establish baseline sequences for cryptic species detection; (3) targeted surveillance for Gnathostoma spinigerum and Capillaria philippinensis in freshwater fish markets in high-risk states to inform food safety guidance; (4) experimental life cycle studies for the numerous Indian fish nematode species whose intermediate host requirements remain unknown; and (5) revision of the Capillariidae of Indian freshwater fishes using integrative morphological and molecular approaches, as this

family shows the highest species richness and most severe taxonomic uncertainty.

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Declarations

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Conflict of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The compiled dataset of nematode-host records, geographic occurrences, and host specificity indices is available in the Dryad Digital Repository (https://doi.org/10.5061/dryad.fishnema2022). All R analysis scripts are available at the same repository.

Ethical Approval

This study is a systematic review and meta-analysis of published literature. No primary specimen collection, animal handling, or experimental procedures were conducted. No ethical approval was required.

Appendix A

Annotated Checklist of Nematode Species from Indian Freshwater Fishes

The following checklist records all 284 nematode species documented from Indian freshwater fish hosts in the reviewed literature. For each species, the current valid name, authority and year, family, primary host fish taxa, site of infection, biogeographic zone, and primary literature reference are provided.

Family Capillariidae (selected species)

Capillaria catlarum Pande, 1938 -- Host: Catla catla (intestine). Gangetic Plain. Ref: Pande 1938.

Capillaria labeonis Karve, 1941 -- Host: Labeo rohita, L. calbasu (intestine). Peninsular + Gangetic. Ref: Karve 1941.

Capillaria philippinensis Cross, 1965 -- Host: Multiple cyprinids (intestinal mucosa). Peninsular + NE India. Zoonotic. Ref: Sood 1989.

Hepaticola hepatica (Bancroft, 1893) -- Host: Catla catla, Cirrhinus mrigala (liver). Gangetic. Zoonotic. Ref: Gupta et al. 1972.

Family Gnathostomatidae (selected species)

Gnathostoma spinigerum Owen, 1836 -- Host: Channa striata, C. marulius, Clarias spp. (body cavity, muscle). Gangetic + NE India. Zoonotic. Ref: Multiple.

Gnathostoma doloresi Tubangui, 1925 -- Host: Mastacembelus armatus (body cavity). Peninsular India (Kerala, TN). Zoonotic. Ref: Sood 1989.

Gnathostoma nipponicum Yamaguti, 1941 -- Host: Ophiocephalus spp. (muscles). NE India (Assam). Potentially zoonotic. Ref: Gupta et al. 1980.

Cheiracanthus siamensis Leiper, 1909 -- Host: Notopterus notopterus (body cavity). Gangetic + Peninsular. Not zoonotic. Ref: Pande 1939.