

Research Paper

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Two new dactylogyrid species (Platyhelminthes: Monogenea) parasitising the gills of *Garra gotyla* (Cyprinidae) in India: morphological and molecular characterization

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Abstract

Garra gotyla is a benthopelagic freshwater cyprinid fish native to Asia, valued for both food and ornamental purposes; nevertheless, its parasitic diseases are poorly understood. The present study investigated the presence and ecological indices (prevalence and intensity) of monogenean parasites infecting *G. gotyla* in Mizoram, northeast India. Additionally, the study aimed to assess the phylogenetic relationships among three closely related dactylogyrid genera: *Dactylogyrus*, *Dogielius*, and *Dactylogyroides*. Monogeneans were initially identified based on the comparative morphology of their sclerotised haptor and reproductive structures, followed by BLASTn comparisons of their partial 28S rRNA gene sequences. Two dactylogyrid species, *Dactylogyrus labro* sp. n. and *Dogielius salpinx* sp. n., were recovered and are described herein as new to science. *Dactylogyrus labro* was found to infect all examined fish, whereas *D. salpinx* had a slightly lower prevalence, ranging from 76.5% to 83.3% across different sampling sites. The phylogenetic insights from these species presented in this study highlight the complex evolutionary relationships within these three genera. Further, this study provides the first confirmed molecular data for a *Dogielius* species, allowing for much-needed phylogenetic studies on the genus and filling a gap in sequencing data for Indian monogeneans. Since all monogeneans are potentially hazardous parasites, more studies are needed to map their diversity and effects on host fishes in this region.

Introduction

Monogenea Van Beneden, 1858, is one of the three parasitic classes within the phylum Platyhelminthes Minot, 1876, the others being Trematoda and Cestoda. Monogeneans are mostly ectoparasites of fish, infecting all major taxa, from primitive Agnatha to Chondrichthyes to Osteichthyes, across freshwater, brackish, and marine environments. They may cause direct losses due to mortality, typically to younger fish and those in intensive culture or captivity (Thoney & Hargis, 1991), by feeding on blood (Hayward *et al.*, 2007) and/or the epithelial cells and mucus of fish (Buchmann & Bresciani, 2006). Since their discovery in the 18th century by the German zoologist Müller (1776), nearly 7000 species have been described (Gibson *et al.*, 2014).

Mizoram, located in northeast India, is recognised as a global biodiversity hotspot (Barman *et al.*, 2018). The region is rich in freshwater fish diversity, with at least 156 recorded species representing nine orders, 26 families, and 72 genera. Of these, approximately 78 species belong to the family Cyprinidae and are distributed across the diverse hilly terrain of the state (Lalhlimpua *et al.*, 2017). Given that parasite species richness is generally positively correlated with host species richness, it is expected that Mizoram will support a diverse range of monogenean species. However, due to limited parasitological research conducted in the region, *Dactylogyrus kolodnyensis* Trivedi, Prakash and Tripathi, 2022 is currently the only monogenean species documented from Mizoram.

Garra gotyla (Gray, 1830) (Cyprinidae, Labeoninae), commonly known as ‘sucker head’, is a benthopelagic species inhabiting the fast-flowing rivers, mountain streams, submerged rocks, and lakes of Asia (Froese & Pauly, 2023). It is one of the most important native ornamental fish species in India (Mandal *et al.*, 2007). Jha *et al.* (2005) reported that a substantial population in Nepal rely on *G. gotyla* as a protein source. Despite its prominence, diseases affecting *G. gotyla* in the region remain largely unexplored, with research primarily focusing on the impact of environmental pollutants (Munir *et al.*, 2021; Sharma & Langer, 2014). Only one species of Monogenea has been documented from the gills of *G. gotyla*, namely *Lobotrema rajendrai*, in north India over half a century ago (Srivastava & Kumar, 1983).

During a recent parasitological investigation in Mizoram, north-east India, two previously undescribed dactylogyrid species were found on the gills of *G. gotyla*. Subsequent morpho-molecular examination confirmed these specimens as novel species, herein described as *Dactylogyrus labro* sp. n. and *Dogielius salpinx* sp. n.

Dactylogyrus, *Dogielius*, and *Dactylogyroides* are three closely related dactylogyrid genera (subclass Polyonchoinea) whose member species are mostly found on cyprinid hosts (Gusev, 1963, 1976; Price & Yurkiewicz, 1968). Of these, *Dactylogyrus* is the most species-rich, with over 1000 nominal species worldwide (WoRMS, 2025), including 58 species from India (Khwaja et al., 2023). Meanwhile, *Dogielius* is found in Africa, China (including the Amur region of Russia), the Indian subcontinent, and parts of Eurasia (Timofeeva et al., 1997), with 43 nominal species globally, including five from India (WoRMS, 2025). On the other hand, *Dactylogyroides* Gusev, 1963 comprises 16 known species distributed across Africa, Ceylon, India, Peninsular Malaysia, Thailand, and China, including seven from India (WoRMS, 2025). The key morphological differences among these genera are summarised in Table 1.

The taxonomic validity and phylogenetic relationships of these three genera have long been a subject of confusion. For example, Musilová et al. (2009) stated that '*Dactylogyrus* and *Dogielius* are morphologically similar genera parasitising many species of the Cyprinidae.... One striking feature that separates these taxa is [that the] *Dactylogyrus* species lost the ventral anchor-bar complex, while *Dogielius* spp. lost the dorsal complex'. Meanwhile, Kritsky et al. (2010) noted that 'the phylogenetic position of *Dogielius* and *Thaparocleidus* (both with freshwater species having ventral anchor/bar complexes) is currently unknown'. More recently, some studies, such as Raphahlelo et al. (2020), assigned some monogenean species to *Dactylogyrus* which, based on illustrations and images, appear to correspond more closely with *Dactylogyroides*.

Table 1. Diagnostic morphological characters distinguishing *Dactylogyrus* Diesing, 1850, *Dogielius* Bychowsky, 1936, and *Dactylogyroides* Gusev, 1963 (Dactylogyridae)

Characters	Genera		
	<i>Dactylogyrus</i>	<i>Dogielius</i>	<i>Dactylogyroides</i>
Anchor			
Number	One pair (dorsal)	One pair (ventral)	One pair (dorsal)
Point orientation	Dorsally directed	Directed towards each other often with a sharp bend,	Dorsally directed
Bar			
Number	Usually one (dorsal)	Always one (ventral)	Always two (dorsal and ventral)
Dorsal bar	Variable in shape	Absent	Two-pieced, V-shaped
Ventral bar	Usually smaller when present	Robust	Stick- to wide U-shaped
Vagina			
Placement	Dextral (rarely sinistral)	Not always confirmed	Not always confirmed
Host			
	Cyprinidae, Catostomidae, Cobitidae	Cyprinidae	Cyprinidae

In fact, one unpublished preprint even proposed synonymising both *Dogielius* and *Dactylogyroides* with *Dactylogyrus* (available at <https://ecoevorxiv.org/repository/view/3947/>).

Against this backdrop, this paper aims to describe and illustrate two new monogenean species found on *G. gotyla* in northeast India while also discussing the phylogenetic relationships among *Dactylogyrus*, *Dogielius*, and *Dactylogyroides*.

Materials and methods

Between March and May 2022, 50 specimens of *G. gotyla* were caught with electrofishing from three locations in the Serchhip District of Mizoram, northeast India: Mat River (23° 16' 33.8" N, 92° 49' 40.1" E), Tuichang River (23° 15' 58.8" N, 92° 57' 07.7" E) and Tuikum River (23° 24' 26.0" N, 92° 53' 07.0" E). Identification and nomenclature of fish followed the method of Nebeshwar and Vishwanath (2013). Before parasitological investigations, individual fish were euthanized with an overdose of sodium bicarbonate-buffered tricaine methane-sulfonate (MS-222 100 mg/L; Sigma Aldrich Co., USA).

Freshly excised gills were examined under a Leica EZ4HD binocular microscope, and any monogeneans spotted were carefully removed using fine dissection needles. These monogeneans were either mounted unstained in a small drop of Hoyer's medium or glycerine or stained with Gomori's trichrome before being mounted in dibutyl phthalate polystyrene xylene (DPX), following the protocols outlined by Kritsky et al. (1986) and Tripathi et al. (2022). The slides were examined using a light microscope (DM4B, Leica Microsystems, Germany) equipped with phase-contrast and differential interference contrast optics and a Leica DFC7000 T digital camera. Composite line drawings were prepared using a drawing tube attachment fixed to a light microscope (BX 51, Olympus, Japan). The prevalence and mean intensity of infection were calculated according to Bush et al. (1997). Type specimens (one holotype and four paratypes of each species) were deposited in the Queensland Museum, Brisbane, Australia.

Individual monogeneans were identified morphologically and pooled by species (>5 individuals). Total genomic DNA was extracted from these pools using the Extracta DNA Prep (Quantabio, Beverly, USA). The variable domains D1-D2 of the 28S rRNA gene were amplified by employing the primer set C1 (5'-ACCCGCTGA ATTTAAGCA-3') and D2 (5'-TGGTCCGTGTTTCAAGAC-3') (Hassouna et al., 1984). The amplification profile was constructed following Šimková et al. (2006). The PCR products were purified with the QIAquick PCR purification kit (Qiagen, USA) and sequenced in both forward and reverse directions using the same primers employed in the amplification. The resulting sequence chromatograms were edited with SnapGene version v5.3 (<http://www.snapgene.com>) and assembled using the DNA Baser Sequence Assembler (2013). The generated sequence contigs were submitted to GenBank and compared with related sequences in the NCBI Database (BLASTn, <https://blast.ncbi.nlm.nih.gov/Blast.cgi>) to achieve species-rank identification.

To ascertain the systematic position of the new species, we conducted phylogenetic analyses. All available 28S rRNA sequences for species of *Dogielius*, *Dactylogyrus*, and *Dactylogyroides* were retrieved from NCBI GenBank (search term 1: "*Dactylogyrus* AND 28S"; search term 2: "*Dogielius* AND 28S"; search performed on 19 May 2025) and converted into a local BLAST database, against which the newly generated partial 28S rRNA sequences were compared using the BLASTn algorithm. All sequences with sequence similarity of more than 80% across an alignment length of

at least 320 bp were included in subsequent analyses, together with the partial 28S rRNA sequences of the new species.

Tetraonchus monenteron (Wagener, 1857) Diesing, 1858 (GenBank: AJ969953) and *Paradiplectanum sillagonum* (Tripathi, 1959) Domingues and Boeger, 2009 (GenBank: AY553626) were included as the outgroups to root the tree, following Roohi *et al.* (2019) and Kmentová *et al.* (2022), respectively.

Sequences were clustered at 100% identity using vsearch v. 2.23.0 (Rognes *et al.* 2016), before multiple sequence alignment was performed using MAFFT v. 7.464 in L-INS-I mode (Katoh & Standley 2013). Alignments were subsequently trimmed using trimAl v. 1.4.1 in gappout mode (Capella-Gutiérrez *et al.* 2009). A maximum-likelihood tree was inferred using IQ-TREE v. 2.0.7 (Nguyen *et al.* 2015) with 1000 ultrafast bootstrap replicates, using the best-fitting model of sequence evolution as determined automatically by ModelFinder as implemented in IQ-TREE. Bayesian inference was performed on the same trimmed data matrix using MrBayes v3.2.6 (Ronquist *et al.* 2012), with the model of evolution set to GTR with gamma-distributed rate variation across sites and a proportion of invariable sites (GTR+I+G; nst=6 rates=invgamma) and two independent MCMC (Markov chain Monte Carlo) runs with four chains each running for up to 10M generations (further relevant MCMC parameters: temp=0.2 mcmcDiagn=yes diagfreq=1000 stoprule=yes stopval=0.01 samplefreq=100 relburnin=yes burninfrac=0.25), with the automatic stopping rule set to ASDSF≤0.01.

In addition to the large dataset, we compiled a smaller dataset comprising a random selection of publicly available sequences from the major clades. Multiple sequence alignment was performed with ClustalW (Thompson *et al.*, 1994) in Molecular Evolutionary Genetic Analysis 11 (MEGA11) software (Tamura *et al.*, 2021). Phylogenetic inferences (ML and BI) were then performed as described above. Genetic distances (uncorrected p-distance) were calculated in MEGA11 (Tamura *et al.*, 2021) based on a reduced (small) dataset represented in the ML tree, with default settings (Rates among Sites: Uniform Rates; Gaps/Missing Data Treatment: Pairwise deletion).

The aligned sequences are provided in [Supplementary Data S1](#) and [S2](#), while the corresponding tree files are available as [Supplementary Data S3](#) (ML tree, NEWICK format) and [S4](#) (BI tree, NEXUS format). Trees based on the reduced dataset are provided in [Supplementary Data S5–S6](#), and a list of sequences comprising the collapsed clades in [Figure 5](#) is provided in [Supplementary Data S7](#).

Results

Morphological characterization

Class Monogenea van Beneden, 1858

Order Dactylogyridea Bychowsky, 1937

Family Dactylogyridae Bychowsky, 1933

Genus *Dactylogyrus* Diesing, 1850

Dactylogyrus labro sp. n.

ZooBank registration: urn:lsid:zoobank.org:act:60304DFF-4D5F-4C42-9C72-62539F4E6C0C

Type host: *Garra gotyla* (Gray, 1830) (Cypriniformes, Cyprinidae)

Type locality: Mat River, Tuichang River, and Tuikum River in Serchhip district, Mizoram, India

Infection site: Gill lamellae

Infection parameters: See [Table 2](#).

Table 2. Prevalence and mean intensity of infection of *Dactylogyrus labro* sp. n. and *Dogielius salpinx* sp. n. from *Garra gotyla* in the present study

Locality	Infection parameters	<i>D. labro</i> sp. n.	<i>D. salpinx</i> sp. n.
River Mat	No. of examined fish	15	15
	No. of infected fish	15	12
	Prevalence (%)	100	80
	Mean intensity	24.2 ± 6.2 (15–35)	16.8 ± 4.7 (10–25)
River Tuichang	No. of examined fish	18	18
	No. of infected fish	18	15
	Prevalence (%)	100	83.3
	Mean intensity	26.1 ± 6.7 (16–38)	14.3 ± 4.4 (8–22)
River Tuikum	No. of examined fish	17	17
	No. of infected fish	17	13
	Prevalence (%)	100	76.4
	Mean intensity	23.2 ± 6.2 (14–34)	12.8 ± 4.1 (7–20)

Type material: Queensland Museum, Holotype, AHC37169; 4 Paratypes, AHC37170–AHC37173

Representative DNA sequence: 28S rRNA (850-bp) (GenBank: OR347559)

Etymology: From the Latin noun *labrum* (= flange), in reference to the presence of a projecting edge at the base of the copulatory tube of this species.

Description (Figures 1 and 2; metrical data in [Table 3](#))

With characters of the genus as defined by Diesing (1850). Single pairs of (dorsal) anchors, with distinct outward bulge on an otherwise evenly curved shaft. Single (dorsal) bar, rod-shaped with very short posteromedial expansion, and downward posterolateral expansions on both ends. Seven pairs of hooks, uniform in shape but diverse in size, each with delicate point, upright thumb, shank of two subunits (proximal subunit significantly expanded), and filamentous hook (FH) loop extending to the near union of shank subunits. Male copulatory complex comprises a male copulatory organ (MCO), accessory piece, and a thick ligament. Male copulatory organ is a loose coil of 1.1/2 clockwise rings and a swollen base with a lateral flange, narrowing to termination. Proximal part of the accessory piece articulates with the base of the copulatory tube through a thick ligament, and the distal part is twisted with a grooved sheath serving as guide for MCO and dorsal ribbon-like sclerotised strap. Vagina tubular, sclerotised, serpentine-coiled, with swollen proximal base and slightly expanded distal end with pore.

Remarks: *Dactylogyrus labro* sp. n. is distinguished from its congeners by the presence of a unique combination of morphological features, including an MCO with 1.1/2 complete clockwise coils with a swollen base bearing a lateral flange, an accessory piece comprising a grooved sheath to guide the MCO, accompanied by a ribbon-like sclerotised strap, and a serpentine, coiled vagina. To the best of our knowledge, the presence of a flange at the base of MCO has not been reported in any other *Dactylogyrus* species and, hence, may represent a diagnostic feature of *D. labro* sp. n.

Class Monogenea Van Beneden, 1858

Order Dactylogyridea Bychowsky, 1937

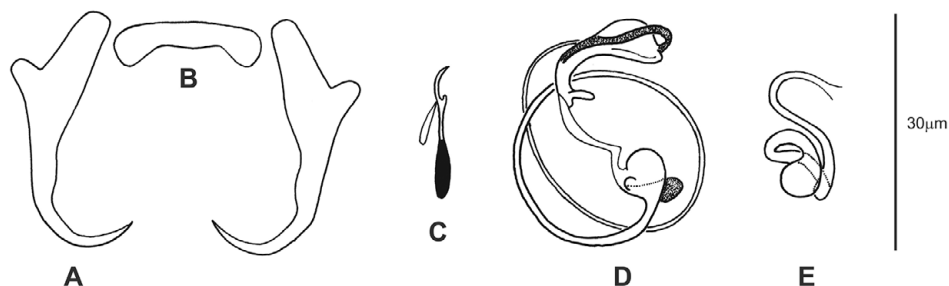


Figure 1. Line drawings of *Dactylogyrus labro* sp. n. from *Garra gotyla* (Gray, 1830). (A) dorsal anchor; (B) dorsal bar; (C) hook (pairs I–VII); (D) male copulatory organ; (E) vagina. Scale bar = 30 µm.



Figure 2. Phase-contrast micrographs of *Dactylogyrus labro* sp. n. from *Garra gotyla* (Gray, 1830). (A) whole mount; (B) anchor-bar complex and hooks; (C) male copulatory organ; (D) vagina. Scale bar = 20 µm.

Family Dactylogyridae Bychowsky, 1933

Genus *Dogieli* Bychowsky, 1936

Dogieli *salpinx* sp. n.

ZooBank registration: urn:lsid:zoobank.org:act:8B8F9CB3-BE2F-440A-A31F-CB7BBDD0A677

Type host: *Garra gotyla* (Gray, 1830) (Cypriniformes, Cyprinidae)
Type locality: Mat River in Serchhip District of Mizoram, northeast India.

Additional localities: Tuichang River and Tuikum River in Serchhip District of Mizoram.

Infection site: Gill lamellae

Infection parameters: See Table 2.

Type material: Queensland Museum, Holotype, AHC 37164; 4 Paratypes, AHC37165–AHC37168.

Representative DNA sequence: 28S rRNA (873 bp) (GenBank: OR347563)

Etymology: From the Greek *salpinx* = a trumpet, in reference to the accessory piece of male copulatory organ.

Description (Figures 3 and 4; metrical data in Table 3)

With traits of the genus as defined by Bychowsky (1936). Single pair of (ventral) anchors, with a deep cleft between two well-developed roots;

point recurved, bent at the end. Single (ventral) bar, wide U-shaped, robust, with medial part slightly twisted forward, extremities nearly bilobed. Seven pairs of hooks, similar in shape but dissimilar in size, each with a delicate point, erect thumb, and a shank of two subunits (proximal subunit expanded), along with a filamentous hook (FH) loop extending to the near union of shank subunits. Male copulatory complex comprises male copulatory organ (MCO) connected to accessory piece by laminar ligament attached to the base of the MCO. Male copulatory organ is straight and robust with inflated base. Accessory piece robust, comprising two subunits; anterior subunit serves as guide for the MCO, posterior subunit is somewhat trumpet-head-shaped, which articulates with the base of MCO via long and thick sclerotised thread. Vagina globular, seed-shaped, with a central slit-like opening, and highly sclerotised, and sinistral; vaginal tube not visible. Egg elongate-oval, shell surface thick, smooth; internal contents granular; no polar filaments or operculum observed.

Remarks: *Dogieli* *salpinx* sp. n. closely resembles *D. kaelensis* Narba, Matey, Tripathi 2022 from *Garra annandalei* Hora, 1921 and *D. catlaius* (Jain, 1962) Gusev, 1976 from *Catla catla* (Hamilton, 1822) (now *Gibelion catla*) in India, in the nearly identical shape and size of their anchors. The proposed new species, however, differs from *D. kaelensis* by possessing a larger ventral bar (66 µm vs 43 µm in *D. kaelensis*), an accessory piece of distinct

Table 3. Measurement data (in μm) for *Dactylogyrus labro* sp. n. and *Dogielius salpinx* sp. n. [presented as range, followed by mean and number (n) of structures measured in parentheses]

Characters	<i>D. labro</i> sp. n.	<i>D. salpinx</i> sp. n.
Haptoral hard parts		
Anchor inner length	24 (23–26)	33 (32–35)
Anchor inner root	13 (12–15; n = 9)	12 (11–15; n = 7)
Anchor outer root	5 (4–6; n = 8)	9 (8–10; n = 7)
Anchor shaft	4 (2–6; n = 7)	–
Anchor point	10 (9–12; n = 8)	–
Dorsal bar length	24 (22–25; n = 10) $\times$ 3 (2–6; n = 7)	–
Ventral bar length	–	66 (65–70; n = 9)
Hook lengths	Pair I–VII: 22 (21–24), 27 (25–28), 27 (25–28), 24 (23–26), 26 (25–27), 13 (12–15), 15 (14–17) (n = 7)	19 (18–31; n = 5)
Reproductive hard parts		
Copulatory tube length	130 (126–132; n = 5)	20 (19–22; n = 8)
Accessory piece length	18 (17–20; n = 7)	13 (12–16; n = 8)
Vagina length	38 (35–40; n = 5)	10 (8–12; n = 7)
Egg diameter	Not observed	47 (43–52; n = 5)

morphology (trumpet-head-shaped vs. a ring-shaped middle part in *D. kaelensis*), and a differently shaped vagina (globular, seed-shaped vs. flower-shaped in *D. kaelensis*). The new species can also be differentiated from *D. catlaius* by the shape of the MCO, which is nearly straight in the new species (curved in *D. catlaius*), and an accessory piece that is trumpet-head-shaped in the new species (pivot-shaped with three processes in *D. catlaius*). This distinct haptoral and reproductive sclerite morphology distinguishes *D. salpinx* sp. n. as a novel species within the genus *Dogielius*.

Molecular characterization

Sequencing of the partial 28S rRNA gene of *D. labro* sp. n. resulted in an amplicon 850 base pairs long. Sequence comparison using a BLASTn search showed no exact matches in GenBank. The species with the closest nucleotide similarity to *D. labro* sp. n. was *D. brevicirrus* Paperna, 1973 from *Labeo parvus* (Boulenger, 1902)

(KY629362; 99% query coverage, 88.62% maximum identity) in Senegal, West Africa, from which the new species differed by 13 gaps (1%) (Table 4). This similarity was confirmed in the phylogenetic tree, where *D. labro* sp. n. clustered with *D. brevicirrus*, *D. senegalensis* Paperna, 1969, and *D. oligospirophallus* Paperna, 1973 (three top BLASTn search matches) with 100% bootstrap support (Figure 5).

Sequencing of the partial 28S rRNA gene of *D. salpinx* sp. n. resulted in an amplicon 873 base pairs long. Sequence comparison using a BLASTn search revealed less than 100% similarity with any of the known sequences in GenBank. The species with the closest nucleotide similarity to *D. salpinx* sp. n. was *D. brevicirrus* from *L. parvus* (KY629362; 97% query coverage, 86.61% maximum identity) in Senegal, West Africa, from which the new species differed by 24 gaps (2%) (Table 4). The average genetic p-distance between *D. labro* sp. n. and other species of *Dactylogyrus* ranged between 11.44% and 21.86%, while that between *D. salpinx* sp. n. and *D. catlaius* was 11.78% (Table 5).

Phylogenetic inference was performed based on partial 28S rRNA sequences obtained for *D. labro* sp. n. and *D. salpinx* sp. n. collected in India, combined with 219 published rRNA sequences, including 217 representatives of the genera *Dactylogyrus*, *Dogielius*, and *Dactylogyroides*, and two outgroup sequences. Maximum likelihood and Bayesian inference (ASDSF = 0.014, APRSF = 1.001, and ESS > 1000 for all parameters after 10M generations) of this dataset yielded congruent topologies, supporting the phylogenetic placement of the new species within a strongly supported clade comprising species infecting cyprinid fishes from Europe, Asia, and Africa (Fig. 5).

Dactylogyrus labro sp. n. and *D. salpinx* sp. n. were found most closely related to *D. oligospirophallus* and *D. tripathii*, respectively, with strong statistical support in ML and BI analyses. The two new species are grouped with species infecting African and Asian cyprinids (subclade A), with the majority of isolates from the subfamily Labeoninae. Notable exceptions were *D. marocanus* (ex. subfamily Torinae), *D. pulcher* (ex. subfamily Barbinae), and *Dactylogyroides tripathii* (ex. subfamily Smiliogastrinae).

Subclade B was dominated by *Dactylogyrus* spp. infecting cyprinids of the subfamily Smiliogastrinae, while subclade C comprised *Dactylogyrus* spp. infecting hosts of subfamilies Cyprininae and Barbinae. Subclade D comprised *Dactylogyrus* spp. isolates primarily from Cyprininae hosts (chiefly *Cyprinus* spp. and *Carassius* spp.), with few isolates reported from Xenocyprinidae. Subclade B was consistently recovered as sister to subclade A in both ML and BI analyses based on the full dataset, albeit with only moderate statistical support; hence, this hypothesis must be considered tentative until further data become available.

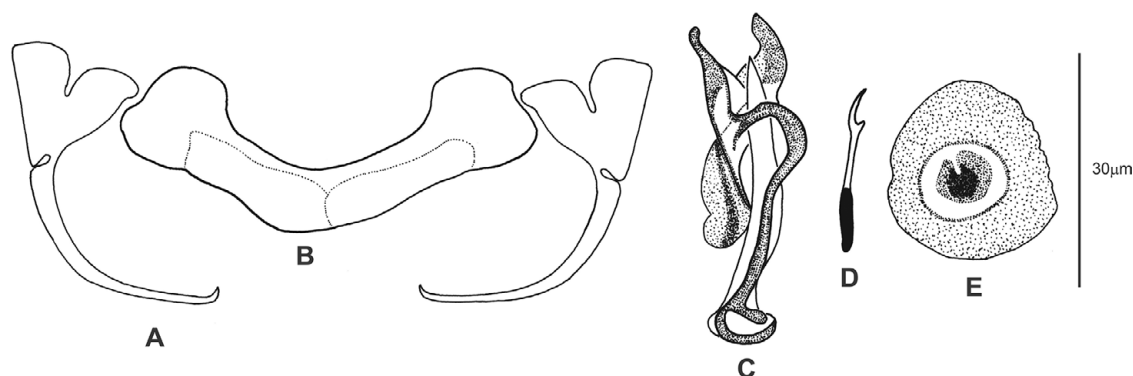


Figure 3. Line drawings of *Dogielius salpinx* sp. n. from *Garra gotyla* (Gray, 1830). (A) ventral anchor; (B) ventral bar; (C) male copulatory organ; (D) hook (pairs I–VII); (E) vagina. Scale bar = 30 μm .



Figure 4. Phase-contrast micrographs of *Dogielius salpinx* sp. n. from *Garra gotyla* (Gray, 1830). (A) whole mount; (B) anchor-bar complex and hooks; (C) male copulatory organ; (D) vagina and egg. Scale bar = 20 μm.

Table 4. Top three BLASTn search matches in GenBank for 28S rRNA gene sequences of *Dactylogyrus labro* sp. n. (850 bp) and *Dogielius salpinx* sp. n. (873 bp)

Monogenean species	Accession no.	Host species	Locality	Query cover identity	
				(%)	(%)
For <i>Dactylogyrus labro</i> sp. n.					
<i>Dactylogyrus brevicirrus</i> Paperna, 1973	KY629362	<i>Labeo parvus</i>	Senegal	99.0	88.6
<i>Dactylogyrus senegalensis</i> Paperna, 1973	KY629363	<i>Labeo senegalensis</i>	Senegal	98.0	88.8
<i>Dactylogyrus oligospirophallus</i> Paperna, 1973	KY629361	<i>Labeo coubie</i>	Senegal	96.0	86.2
For <i>Dogieliu salpinx</i> sp. n.					
<i>Dactylogyrus brevicirrus</i> Paperna, 1973	KY629362	<i>Labeo parvus</i>	Senegal	97.0	86.6
<i>Dactylogyrus</i> sp. q JD–2022	OP419547	<i>Semilabeo obscurus</i>	China	87.0	88.0
<i>Dactylogyrus titus</i> Guegan, Lambert & Euzet, 1988	KY629364	<i>Labeo senegalensis</i>	Senegal	98.0	86.0

Subclades C and D were not recovered in the analyses based on our reduced dataset (Supplementary Data S5–S6), indicating that limited taxon sampling may affect their inferred branching order. While the higher-level relationships in the genus *Dactylogyrus* are not the focus of the current study and will therefore not be discussed further, the branching order of the remaining clades appears robust and strongly supported in both ML and BI analyses of the full dataset (Figure 5) and is in agreement with a recent study (Nitta et al., 2023). It is noteworthy, however, that sequences previously deposited as *D. catlaius* are consistently recovered at a basal position across all analyses.

Discussion

This study presents two new dactylogyrid species in the gills of *G. gotyla* in Mizoram: *D. labro* sp. n. and *D. salpinx* sp. n. Morpho-molecular comparisons with other closely related species confirmed the validity and placement of these two taxa within *Dactylogyrus* and *Dogielius*. Surprisingly, we did not find any evidence of *L. rajendrai* infection in any of the sampled host specimens. While epidemiological studies were not conducted, the high prevalence of two monogenean species suggests that these parasites may represent a significant risk to fish health in northeast India. As such,

more experimental efforts are required to map the diversity of monogenean parasites and explore their impacts on the health of their host fishes in this region. Such research is especially necessary given that all monogeneans are potentially hazardous fish parasites. According to our phylogenetic results, *D. salpinx* sp. n. and *D. labro* sp. n. were placed into a strongly supported clade (100% bootstrap support) primarily comprising *Dactylogyrus* spp. from labeonin cyprinids, alongside *D. tripathii* from smiliogastrin cyprinids (Figure 5, subclade A). *Dogielius salpinx* sp. n. was found to be a sister species to *D. tripathii*, indicating a closer relationship between *Dogielius* and *Dactylogyroides* than between *Dogielius* and *Dactylogyrus*. This relationship was supported by a lower genetic distance (16.80%) between *Dogielius* and *Dactylogyroides* compared to *Dogielius* and *Dactylogyrus* (14.15%–22.36%) (Table 5). Surprisingly, the sequence previously deposited for *D. catlaius* did not cluster with any of the main clades, not even subclade A, which includes *D. salpinx* sp. n. Rather, it diverged first (100% bootstrap support). A major limitation in accessing the potential synonymy among the genera *Dogielius*, *Dactylogyroides*, and *Dactylogyrus* is the lack of high-quality, morpho-taxonomically validated reference sequences for *Dogielius* and *Dactylogyroides* in GenBank. For *Dactylogyroides*, only five 28S rRNA gene sequences are available, of which just one has been formally published (*Dactylogyroides tripathii*, JX993982; Chiary et al., 2013). Moreover, only two of these sequences exceed

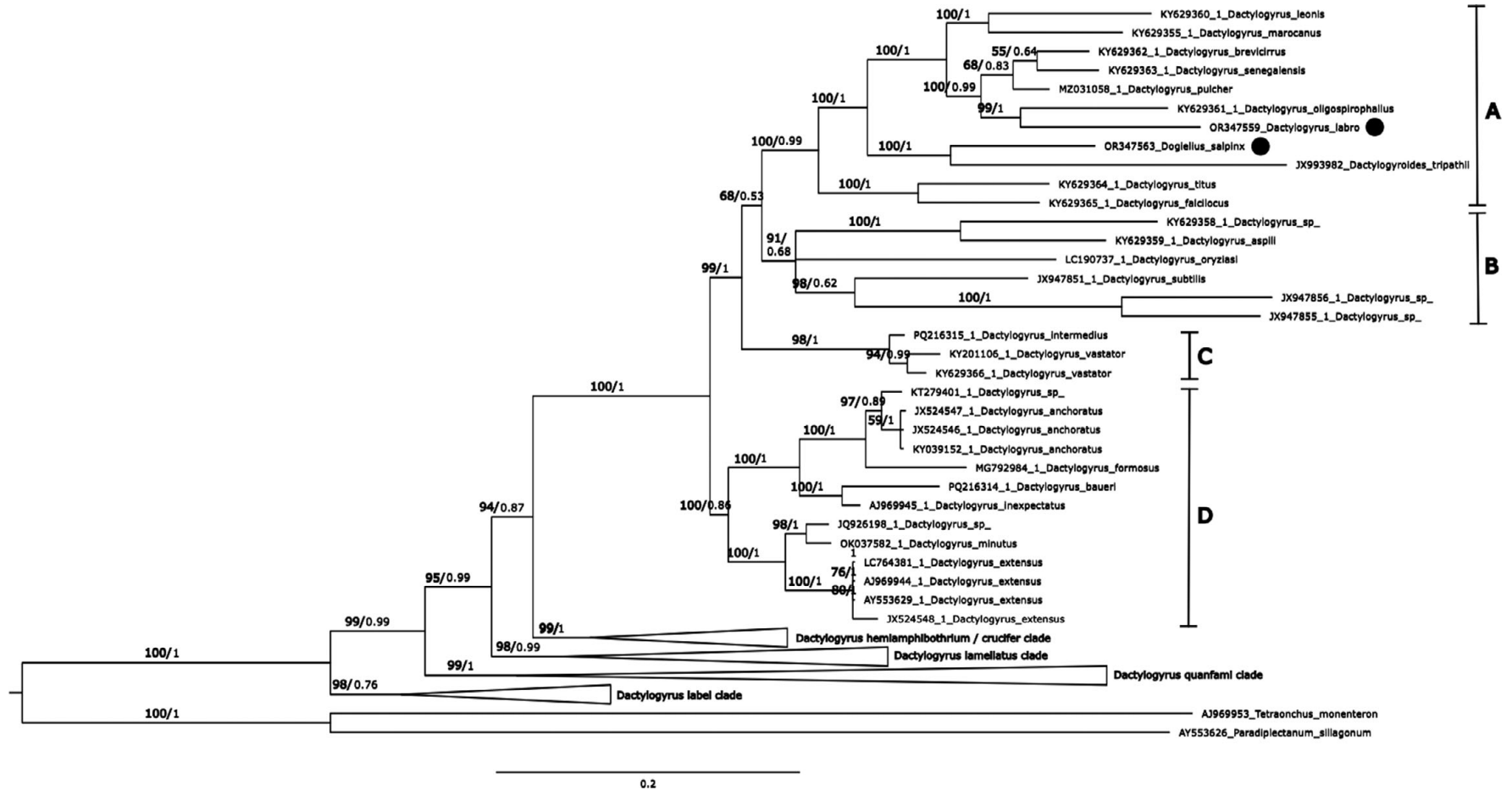


Figure 5. Rooted phylogenetic tree inferred from all available 28S rRNA sequences of *Dactylogyrus* spp., *Dogielius* spp., and *Dactylogyroides* spp. with sequences generated in the present study marked with solid circles. Node support is shown as posterior probability for Bayesian inference (BI) and bootstrap values (from 1000 replicates) for maximum likelihood (ML).

Table 5. A distance matrix viewer for uncorrected pairwise genetic p-distance based on partial 28S rDNA sequences included in the phylogenetic analysis based on a reduced (small) dataset. Newly sequenced taxa are in **bold**

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
1. KY629362	<i>Dactylogyrus brevicirrus</i>																					
2. KY629363	<i>Dactylogyrus senegalensis</i>	0.0504																				
3. KY629361	<i>Dactylogyrus oligospirophallus</i>	0.108	0.0999																			
4. JX524547	<i>Dactylogyrus anchoratus</i>	0.1543	0.145	0.1688																		
5. MG792984	<i>Dactylogyrus formosus</i>	0.2023	0.1882	0.2033	0.0389																	
6. KY629366	<i>Dactylogyrus vastator</i>	0.1865	0.1903	0.2064	0.1245	0.1694																
7. JX524548	<i>Dactylogyrus extensus</i>	0.1551	0.1402	0.1698	0.1151	0.1276	0.1047															
8. OK037582	<i>Dactylogyrus minutus</i>	0.1523	0.1376	0.1667	0.1032	0.1162	0.0971	0.0468														
9. KY629375	<i>Dactylogyrus wunderi</i>	0.2026	0.2026	0.2266	0.1404	0.1676	0.1684	0.1564	0.1358													
10. MG792953	<i>Dactylogyrus zandti</i>	0.1964	0.1951	0.2266	0.1418	0.1943	0.1649	0.152	0.1363	0.0114												
11. KY629374	<i>Dactylogyrus crucifer</i>	0.1938	0.19	0.2151	0.1418	0.1917	0.1637	0.152	0.1363	0.0314	0.0456											
12. MG793023	<i>Dactylogyrus fallax</i>	0.2036	0.1985	0.2261	0.1506	0.2003	0.1645	0.1495	0.1376	0.047	0.0544	0.0342										
13. KY629373	<i>Dactylogyrus suecicus</i>	0.1962	0.1936	0.2225	0.1508	0.1992	0.1686	0.1592	0.1434	0.0428	0.0469	0.0342	0.0266									
14. LC414156	<i>Dactylogyrus skrjabini</i>	0.2019	0.2033	0.2114	0.158	0.1952	0.1994	0.166	0.1648	0.1463	0.1357	0.1357	0.1326	0.1357								
15. LC538183	<i>Dactylogyrus petruschewskyi</i>	0.1995	0.2008	0.2273	0.1617	0.2179	0.1956	0.1604	0.1557	0.1375	0.1279	0.124	0.1301	0.1304	0.0479							
16. MG825765	<i>Dactylogyrus suchengtaii</i>	0.2134	0.209	0.2203	0.1634	0.202	0.2061	0.1677	0.1599	0.1418	0.1371	0.1328	0.1338	0.1328	0.0434	0.0556						
17. KC687091	<i>Dogielius catlaius</i>	0.1456	0.1384	0.1557	0.1108	0.1349	0.1108	0.1	0.0978	0.1148	0.0986	0.104	0.0983	0.104	0.0879	0.0888	0.1027					
18. JX993982	<i>Dactylogyroides tripathii</i>	0.1959	0.1945	0.2196	0.1835	0.2239	0.223	0.2089	0.196	0.2212	0.2373	0.2444	0.238	0.2341	0.2315	0.2422	0.2299	0.1174				
19. OR347559	<i>Dactylogyrus labro sp.n.</i>	0.1198	0.1144	0.1321	0.1698	0.2052	0.2052	0.1645	0.1706	0.2101	0.2063	0.2105	0.2112	0.2019	0.2172	0.2186	0.2174	0.125	0.189			
20. OR347563	<i>Dogielius salpinx sp.n.</i>	0.1493	0.1557	0.166	0.1415	0.1893	0.1945	0.1501	0.1455	0.2125	0.2165	0.2152	0.2225	0.2163	0.2174	0.2263	0.2222	0.1178	0.168	0.178		
21. AY553626	<i>Paradipectanum sillagonum</i>	0.4035	0.399	0.3915	0.3214	0.3926	0.3868	0.3358	0.3278	0.3779	0.3792	0.3792	0.3744	0.3688	0.3463	0.3643	0.3522	0.2308	0.3891	0.3715	0.4008	
22. AJ969953	<i>Tetraonchus monenteron</i>	0.3192	0.3192	0.3386	0.2987	0.3461	0.3503	0.2948	0.283	0.3366	0.3339	0.3397	0.3281	0.3302	0.3333	0.3286	0.3339	0.1917	0.357	0.3339	0.3593	0.313

381 bp in length, thereby limiting their utility for robust phylogenetic inference.

The situation is even more complex for *Dogielius*. GenBank lists two distinct datasets: a single 28S rRNA sequence (KC687091; Dash *et al.*, 2014) for *Dactylogyrus catlaius* Jain, 1961—a species reassigned to *Dogielius* by Gusev (1976)—and 22 sequences (MW479163–MW479184; Paul and Sahoo, 2022), all labelled as *Dogielius catlaius* isolates despite being described as *Dactylogyrus catlaius* in the corresponding publication. All 23 sequences originate from a single laboratory and lack independent taxonomic validation.

Dash *et al.* (2014) identified *D. catlaius* from *Labeo rohita* (Hamilton, 1822) (Cyprinidae), an atypical host, using only 'a light microscopy image at 10x magnification'—an approach insufficient for definitive species-level morphological identification in monogeneans. Similarly, Paul and Sahoo (2022) reported *D. catlaius* from three unrelated cyprinid hosts: *Labeo rohita*, *Catla catla*, and *Cirrhinus mrigala* (Hamilton, 1822). Notably, neither study provided diagnostic-quality microscopic images or the line drawings of the specimens identified as *D. catlaius*, nor did they deposit voucher material in any recognised museum collection, further limiting the verifiability of their identifications.

In both studies, DNA was extracted from the host tissues (gills/mucus) rather than from isolated, morphologically confirmed parasites. This introduces a high risk of contamination from co-infecting taxa and increases the chances of misidentification, especially since *L. rohita* is known to host at least five monogenean genera: *Dactylogyrus*, *Dogielius*, *Gyrodactylus* von Nordmann, 1832, *Mazocraes* Hermann, 1872, and *Paramazocraes* Tripathi, 1959 (Pandey & Agarwal, 2008; Sailaja *et al.*, 2016). Furthermore, the sequence submitted by Dash *et al.* (2014) is 100% identical to a sequence labelled as *D. labei* (JX566720.1) from *C. catla*, indicating a potential misidentification and highlighting the need for critical re-evaluation of these sequences.

Collectively, these findings suggest that none of the sequences currently submitted to GenBank under the name *Dogielius* are taxonomically reliable. This likely explains the anomalous basal placement of *D. catlaius* in our phylogenetic analysis. If the sequence of Dash *et al.* (2014) truly represented a *Dogielius* species, it would be expected to cluster as a sister taxon to *Dogielius salpinx* sp. n. The present study thus provides the first phylogenetically informative 28S rRNA sequence for *Dogielius*, generated from morphologically identified specimens using standard molecular protocols.

Our study supports the view that *Dactylogyrus*, in its traditional circumscription, should continue to be considered paraphyletic (see Aguiar *et al.*, 2017; Benovics *et al.*, 2018, 2021; Kmentová *et al.*, 2022; Ondračková *et al.*, 2023; Hao *et al.*, 2023), with species from two other genera (*Dogielius* and *Dactylogyroides*) nested within it. While additional molecular sequences of the two latter genera are required for their generic status to be tested, this study provides the first confirmed molecular data on *Dogielius* spp., representing a step towards establishing a molecular taxonomic reference library for this genus. Although the pathogenic implications of *D. salpinx* sp. n. and *D. labro* sp. n. are currently unknown, their discovery highlights the unmarked diversity of fish parasites in Mizoram, India.

Conclusion

This study reports the discovery and description of two new monogenean species, *Dactylogyrus labro* sp. n. and *Dogielius salpinx* sp. n., parasitising the gills of *Garra gotyla* in Mizoram, northeast India.

This region has high freshwater biodiversity yet limited parasitological investigations. Morphological examination, combined with partial 28S rRNA gene sequencing, confirmed the distinctiveness and novelty of both species. Phylogenetic analyses placed *D. labro* sp. n. and *D. salpinx* sp. n. within a well-supported clade of *Dactylogyrus* spp. infecting African and Asian Labeoninae hosts, consistent with established patterns of host–parasite co-evolution in monogeneans. *Dogielius salpinx* sp. n. was recovered as sister to *D. tripathii*, indicating a closer evolutionary relationship between *Dogielius* and *Dactylogyroides*. Notably, *D. catlaius* was consistently recovered in a basal position across all analyses, suggesting either unresolved generic boundaries within the *Dactylogyrus*–*Dogielius* complex or, more likely, that the available sequences currently attributed to *D. catlaius* are unreliable. While this study highlights ongoing confusion in the systematics of *Dactylogyrus*, *Dogielius*, and *Dactylogyroides*—compounded by the paucity of high-quality reference sequences for the latter two—it supports the prevailing view that *Dactylogyrus* is paraphyletic, with species of *Dogielius* and *Dactylogyroides* nested within it. These findings emphasise the urgent need for expanded molecular sampling and integrated taxonomic approaches to resolve the complex evolutionary relationships within this hyper-diverse genus.

Supplementary material. The supplementary material for this article can be found at <https://doi.org/10.1017/S0022149X25100813>.

Data availability statement. The parasite materials that support this study are available at the Queensland Museum. Sequence data generated in this study are publicly available in GenBank.

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Author contribution. SP, AKT, SS: conceptualisation, funding acquisition, data collection and analysis, and figure preparation. AT, SS: writing the original draft of the manuscript. CH, AT: phylogenetic analysis and interpretation of molecular data. All authors approved the final draft of the manuscript for publication.

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Competing interests. The authors declare no conflicts of interest.

Ethical standard. All procedures involving live fish were conducted in accordance with relevant guidelines and regulations, with permission from the Directorate of Fisheries, Government of Mizoram, India [Permit No. C.15015/1/2021–DTE(FY)].

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