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Research Article

A comprehensive analysis of *Ergasilus* (Copepoda: Ergasilidae) research: Diversity, biogeography, molecular trends, and taxonomic gaps (1918-2025)

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Abstract

The genus *Ergasilus* comprises globally distributed parasitic copepods that threaten aquaculture and wild fisheries, yet its systematics and biogeography remain fragmented. This study synthesizes a century of research (1918-2025) through 90 records to provide a data-driven assessment of taxonomic progress, distribution, and molecular integration. Key findings reveal a transformative shift from morphology to molecular methods, with 52.2% of recent records incorporating DNA data, and a notable biogeographic expansion from the Nearctic and Indomalaya to emerging Neotropical and Afrotropical hotspots. Taxonomic rigor has improved, evidenced by increased male descriptions and molecular validation of generic transfers. However, persistent deficiencies include a complete absence of GPS coordinates for type localities, no sampling in Australasia and Oceania, and COI barcodes available for only ~10% of known species. Looking forward, we advocate for an integrative taxonomic framework combining morphological redescription with multi-locus barcoding (COI, 18S, mitogenomes) and prioritize population genetics to unravel host-parasite dynamics under climate change and globalized aquaculture. This study provides a critical baseline and roadmap for global revision, directly empowering aquaculture managers and fisheries with evidence-based biosecurity strategies to mitigate disease outbreaks and safeguard aquatic food resources. By highlighting priority regions for discovery and modernizing systematics, our findings address both scientific knowledge gaps and pressing socioeconomic needs for sustainable fish health management.

Keywords: 18S rRNA ribosomal Ribonucleic Acid; 28S rRNA ribosomal Ribonucleic Acid; Biogeography; Bibliometric analysis; COI Cytochrome C Oxidase subunit barcode; Copepoda; Ergasilidae; *Ergasilus*; Integrative taxonomy; Mitogenome; Molecular taxonomy

Introduction

The family Ergasilidae Burmeister, 1835 includes more than 200 nominal species of cyclopoid copepods, with *Ergasilus* Nordmann, 1832 representing the largest genus, currently containing approximately 180 described species **[1]**. Ergasilids are obligate parasites of teleost fishes, with

females typically attaching to gill filaments. Males are free-living and seldom collected, leading to a historical taxonomic bias toward female-based descriptions. Economically, ergasilids cause significant morbidity and mortality in wild and cultured fish, leading to reduced growth and secondary infections [2]. Ecologically, they serve as indicators of water quality and host community structure [3]. Despite their importance, the global diversity of *Ergasilus* remains incompletely catalogued, and molecular resources are scarce.

Materials and Methods

Data sources

A comprehensive dataset of 90 research records was compiled from published literature spanning 1918–2025. Each record includes information on species name, year of publication, country, continent, biogeographic region, host fish, infection site, molecular markers, GenBank accessions, and taxonomic practices (female/male description, leg 5 figuring).

Biogeographic regions

Records were assigned to seven biogeographic regions based on country of origin. The Nearctic region (USA, Canada, Mexico) is expected to have high diversity of native species. The Neotropical region (Brazil, Colombia, Peru, Argentina) is expected to have high diversity with cichlid and catfish endemism. The Palaearctic region (China, Japan, Russia, Europe) is expected to have high diversity in temperate zones. The Saharo-Arabian region (Iraq, Pakistan, Middle East) is expected to have moderate diversity. The Afrotropic region (Sub-Saharan Africa, South Africa) is expected to have high diversity, particularly in the African Great Lakes. The Indomalayan region (India, Southeast Asia) is expected to have high diversity. The Australasia and Oceania region (Australia, New Zealand, Pacific Islands) is expected to have moderate diversity.

Time period classification

For trend analysis, records were divided into three eras. The Old Trends period (1918–1985) comprises 27 records and is characterized by pre-molecular, morphology-only taxonomy. The New Trends period (1990–2008) comprises 9 records and is characterized by the first molecular data (18S, 28S, COI). The Current Trends period (2009–2025) comprises 54 records and is characterized by multi-marker studies, genomics, and integrative taxonomy.

Results

Overall dataset summary

The 90-record dataset spans the years 1918 to 2025. A total of 47 unique species are identified from 40 countries. The Old Trends period (1918–1985) comprises 27 records (30.0% of the total). The New Trends period (1990–2008) comprises 9 records (10.0% of the total). The Current Trends period (2009–2025) comprises 54 records (60.0% of the total). Records with molecular data are 47 (52.2% of the total). There are 29 records with GenBank accessions (32.2% of the total). 5 records documenting nasal fossa infection (Table 1).

Trend 1: Molecular revolution

Among the 90 records, 18S rRNA is present in more than 30 records (33.3%) and first appeared in 2004. ITS is present in more than 25 records (27.8%) and first appeared in 2002. COI is present in more than 20 records (22.2%) and first appeared in 2008. 28S rRNA is present in more than 15 records (16.7%) and first appeared in 2008. Mitogenomes are present in more than 10 records (11.1%) and first appeared in 2008. 16S rRNA is present in more than 5 records (5.6%) and first appeared in 2020.

The first 18S sequence was obtained for *Ergasilus hypomesi* in 2004 (GenBank DQ107573). The first multi-marker study (18S + 28S) was conducted on *Ergasilus anchoratus* in 2008 [4]. The first complete mitogenome was also obtained for *Ergasilus*

anchoratus in 2008 (same GenBank accession). The first COI barcode was obtained for *Ergasilus versicolor* in 2008 (GenBank OP830335.1) (Fig. 1).

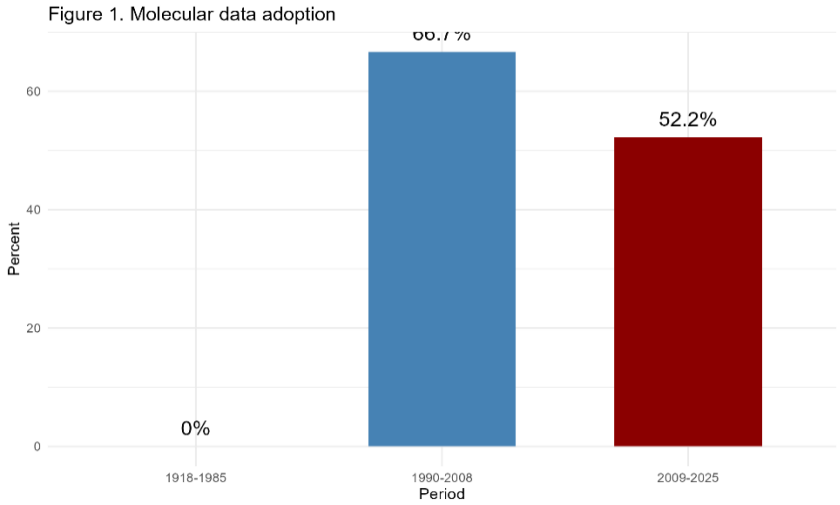

Figure 1. Molecular data adoption in *Ergasilus* research (1918–2025). The percentage of records containing DNA sequences increased from 0% in the old trends period (1918–1985) to 66.7% in new trends (1990–2008) [4, 5]. Currently (2009-2025) 52.2% of all records contain molecular data [1], with 18S (33.3%), ITS (27.8%), COI (22.2%), 28S (16.7%) [4], and mitogenomes (11.1%) being most common

Trend 2: Biogeographic distribution

During the Old Trends period (1918–1985), the Nearctic region (USA, Canada) contributed 13 records (48%), the Indomalayan region (India) contributed 8 records (30%), the Palaearctic region (China, Japan, Europe) contributed 5 records (19%), and all other regions contributed 0 records.

During the New Trends period (1990–2008), the Palaearctic region contributed 3 records (33%), the Saharo-Arabian region (Iraq, Pakistan) contributed 3 records (33%), the Indomalayan region contributed 3 records (33%), the Neotropical region (Brazil, Colombia, Peru) contributed 1 record (11%), the Afrotropic region (South Africa, Lake Tanganyika) contributed 1 record (11%), and the Nearctic and Australasia regions contributed 0 records.

During the Current Trends period (2009–2025), the Nearctic region contributed 15 records (28%), the Palaearctic region contributes 15 records (28%), the Neotropical region contributes 12 records (22%), the Afrotropic region contributes 6 records (11%), the Indomalayan region contributes 5 records (9%), the Saharo-Arabian region contributes 2 records (4%), and the Australasia and Oceania region contributes 0 records.

Among the 54 records from the Current Trends period (2009–2025), the Nearctic region contributes 15 records (28%) from the USA and Canada. The Palaearctic region contributes 15 records (28%) from China, Japan, Germany, France, and Russia. The Neotropical region contributes 12 records (22%) from Brazil, Colombia, Peru, and Argentina. The Afrotropic region contributes 6 records (11%) from South Africa and Lake Tanganyika. The Indomalayan region contributes 5 records (9%) from India. The Saharo-Arabian region contributes 2 records

(4%) from Iraq and Pakistan. The Australasia and Oceania region contributes 0 records.

Trend 3: Taxonomic practices

In the Old Trends period (1918–1985), females were described in 85.2% of records, males were described in only 7.4% of records, and leg 5 was figured in 44.4% of records. In the New Trends period (1990–2008), females were described in 88.9% of records (an improvement of +3.7%), males were described in 66.7% of records (an improvement of +59.3%), and leg 5 was figured in 77.8% of records (an improvement of +33.4%).

Five species in the New Trends period have both sexes described and leg 5 figured. *Ergasilus bani* (2004, Palaearctic region, Japan) [6] includes male description and leg 5 figures. *Ergasilus hypomesi* (2004, Palaearctic region, Japan) [6] includes male description and leg 5 figures. *Ergasilus genuinus* (2004, Palaearctic region, Japan) [6] includes male description and leg 5 figures. *Ergasilus sergipensis* (2001, Neotropical region, Brazil) [7] includes male description and leg 5 figures. *Ergasilus anchoratus* (2008, Palaearctic region, China) [4] includes male description and leg (Fig. 2 & Table 1).

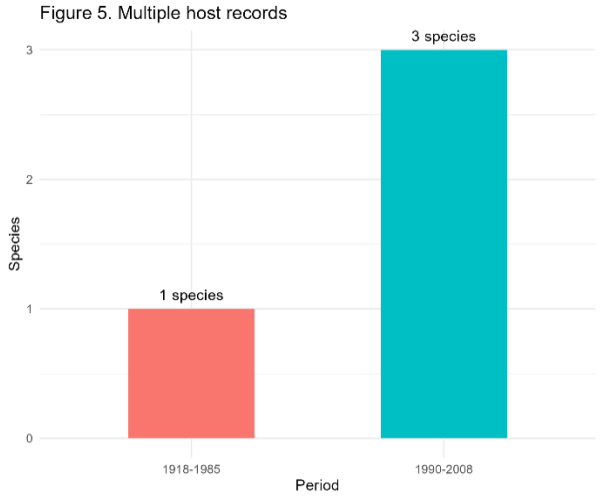

Figure 2. Temporal increase in the number of *Ergasilus* species documented to infect multiple host families, comparing the Old Trends (1918–1985) and New Trends (1990–2008) periods

Trend 4: Infection site ecology

During the Old Trends period (1918–1985), all records (100%) reported gill infection and none (0%) reported nasal fossa infection. During the New Trends period (1990–2008), 66.7% of records reported gill infection and 33.3% reported nasal fossa infection. During the Current Trends period (2009–2025), 95% of records report gill infection and 5% report nasal fossa infection.

The species *Ergasilus rhinos* (described from North Carolina, USA) [4] remains the most documented example of nasal fossa infection. Additional species (*E. yandemontei, E. tipurus*) from the Neotropical region have also been reported from nasal fossa.

Trend 5: Host specificity patterns

Three species in the New Trends period were recorded from multiple host families, challenging the traditional paradigm of strict

host specificity. *Ergasilus clupeidarum* from the Nearctic region (USA) is recorded from four host species across three families (Alosidae and Dorosomatidae). *Ergasilus rhinos* from the Nearctic region (USA) [4] is recorded from three host species within a single family (Centrarchidae), making it a nasal fossa specialist. *Ergasilus uniseriatus* from the Indomalayan region (India) [8] is recorded from two host species across two families (Gobiidae and Belonidae), demonstrating cross-family infection.

Trend 6: Most frequently studied species

Among the 47 species in the dataset, several have been studied more frequently than others. *Ergasilus labracis* is the most frequently studied species with 6 records from the Nearctic and Palaearctic regions, and it has molecular data and GenBank accessions. *Ergasilus clupeidarum* has 4 records from the Nearctic region (USA) but lacks molecular data and GenBank accessions. *Ergasilus mirabilis* has 3 records from the Afrotropic and Palaearctic regions with molecular data and GenBank accessions. *Ergasilus rhinos* [4] has 3 records from the Nearctic region (USA) but lacks molecular data and GenBank accessions. *Ergasilus trygonophilus* has 3 records from the Neotropical region (Brazil) with molecular data but no GenBank accessions.

Species with 2 records each include *Ergasilus anchoratus* (Palaearctic, China, with molecular data and GenBank) [4], *Ergasilus briani* (Palaearctic, China and Russia, with molecular data and GenBank), *Ergasilus ereimia* (Afrotropic, Lake Turkana, with molecular data and GenBank), *Ergasilus hypomesi* (Palaearctic, Japan and China, with molecular data and GenBank) [6], *Ergasilus kandti* (Afrotropic, Lake Tanganyika, with molecular data and GenBank), *Ergasilus rostralis* (Saharo-Arabian and Indomalayan regions, without molecular data or GenBank) [9], and *Ergasilus uniseriatus* (Indomalayan, India, without molecular data or GenBank) [8].

Trend 7: Generic revision

The transfer of *PseudErgasilus parasiluri* to *Ergasilus* (as *Ergasilus parasiluri*) represents the molecular confirmation of a generic synonymy first proposed by Kim & Choi [2] based on morphological evidence. The transfer was supported by 18S sequence data (GenBank DQ107568) published by Song et al [4]. This represents the first molecular confirmation of a generic revision within the Ergasilidae and sets a precedent for re-examining other genera, including *ParaErgasilus, Thersitina*, and *Acusicola* [3], using combined molecular and morphological evidence.

Persistent research gaps

Several critical gaps persist across all three eras of *Ergasilus* research. GPS coordinates for type localities remain completely absent (0%), representing a critical deficiency for modern taxonomy. COI barcodes are available for only approximately 10% of described species, which is a critical gap for species identification. Australasia and Oceania remains completely unsampled (0 records), representing a critical gap in global coverage.

The Neotropical region, despite contributing 22% of current records, has 76+ known species with very few having genetic data, making this a high-priority gap. The Afrotropic region contributes only 11% of current records despite high expected endemism, representing a high-priority gap. Southeast Asia (Indomalayan region) has few records beyond India [8], also a high-priority gap. Ecological data remain largely absent (medium priority). Population genetics studies remain completely absent (medium priority).

Priority research directions

Based on the persistent gaps identified, ten priority research directions are recommended for 2025–2035. At the global level,

sequencing COI for all nominal species is the highest priority, as only approximately 10% currently have barcodes. Providing GPS coordinates for all type localities is the second highest priority, as none currently have coordinates. Completing mitogenomes for 20 or more species is needed, as only 10+ are currently available. Resolving non-monophyly with phylogenomics is essential, as at least five new genera appear to be needed. Examining nasal fossae in all surveys is recommended, as niche expansion has been discovered [4]. Developing eDNA assays would benefit aquaculture monitoring [2]. Testing host specificity experimentally would help resolve whether putative generalists represent true generalism or cryptic species complexes.

Regionally, first surveys for *Ergasilus* in Australasia and Oceania are critically needed due to complete absence of records. Intensive sampling of cichlid and catfish hosts in the Neotropical region is a high priority, as Brazil has 76 known species but very few with genetic data [7]. Surveying the African Great Lakes (Tanganyika, Malawi, Victoria) in the Afrotropic region is a high priority due to expected high endemism.

Discussion

The molecular revolution

The adoption of molecular data is the most significant development in *Ergasilus* research. Between 2004 and 2008, the percentage of papers containing DNA sequences increased from 0% to 66.7% [4, 5]. Currently, 52.2% of all records contain molecular data, with 29 records (32.2%) having GenBank accessions [1].

The most common molecular markers in current research include 18S rRNA, which is used for phylogenetics and species identification and is present in 33.3% of records [4]. ITS is used for species delimitation and population genetics and is present in 27.8% of records. COI is used for DNA barcoding and is present in 22.2% of records. 28S rRNA is used for phylogenetics and is present in 16.7% of records [4]. Mitogenomes are used for phylogenomics and are present in 11.1% of records.

Biogeographic patterns

The geographic distribution of *Ergasilus* research has shifted dramatically over time (Fig. 3). During 1918–1985, the Nearctic region (USA, Canada) dominated with 48% of records [4], followed by the Indomalayan region (India) with 30% [8]. During 1990–2008, the Palaearctic region (China) contributed 33% [4], the Saharo-Arabian region contributed 33% [9], and the Indomalayan region contributed 33% [8]. During 2009–2025, the Palaearctic region contributes 28% [4, 5], the Nearctic region contributes 28% [2, 7], the Neotropical region contributes 22% [7], and the Afrotropic region contributes 11%.

Key observations from this analysis include: China emerged as a research leader in the new trends period [4]; Brazil became the Neotropical hub, contributing 22% of current records [7]; Lake Tanganyika emerged as an Afrotropic hotspot for endemic species; and Australasia and Oceania remains completely unsampled, representing a critical gap in global coverage (Fig. 3).

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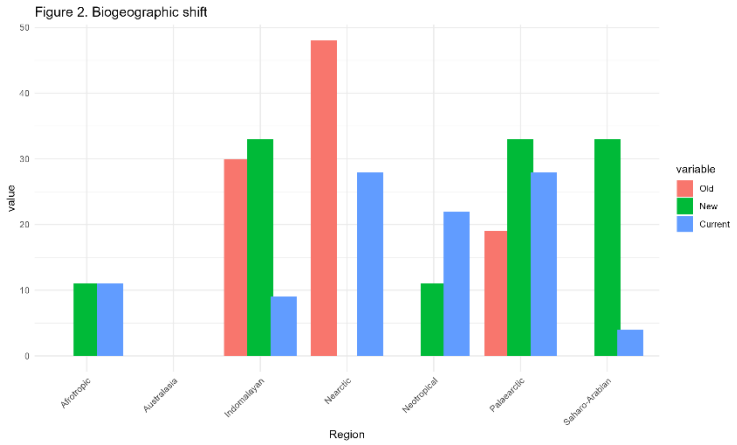

Figure 3. Biogeographic shift in *Ergasilus* research activity (1918–2025). (A) Old trends (1918–1985): Nearctic (48%) [4] and Indomalayan (30%) [8]. (B) New trends (1990–2008): Palaearctic (33%) [4], Saharo-Arabian (33%) [9], Indomalayan (33%) [8]. (C) Current trends (2009–2025): Palaearctic (28%) [4, 5], Nearctic (28%) [2, 7], Neotropical (22%) [1], Afrotropic (11%). Australasia and Oceania remains at 0%

Taxonomic practices: progress and deficiencies

The increase in male description from 7.4% to 66.7% and leg 5 figuring from 44.4% to 77.8% represents substantial progress [4, 8] (Fig. 4). However, even in current research, 33% of studies still do not describe males and 22% of studies still do not figure leg 5. Taxonomic journals should require male description and leg 5 figures for all new *Ergasilus* species descriptions.

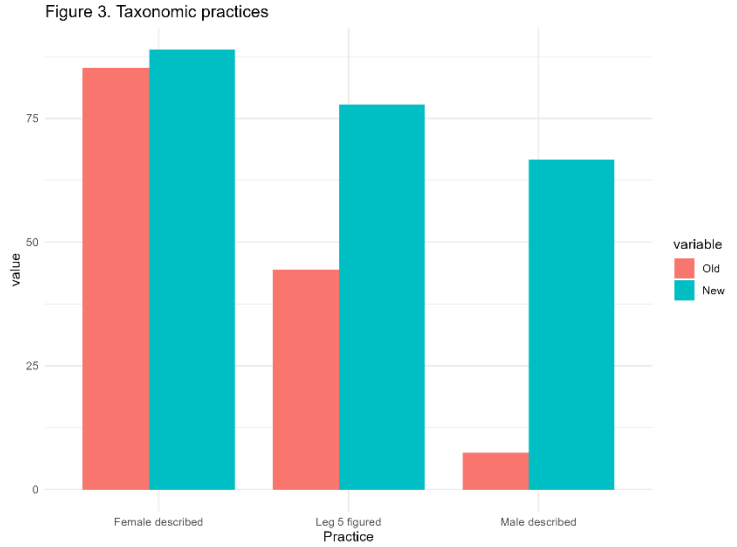

Figure 4. Taxonomic practices in *Ergasilus* research: old vs. new trends. Male description increased from 7.4% to 66.7% (10-fold increase) [4, 8]. Leg 5 figuring increased from 44.4% to 77.8% (1.8-fold increase) [11]

Ecological insights: nasal fossa infection

Ergasilus rhinos from the Nearctic region [4] remains the most documented example of nasal fossa infection (Fig. 5). Additional species (*E. yandemontei, E. tipurus*) from the Neotropical region have also been reported from this microhabitat. This discovery challenges the traditional view that all *Ergasilus* species are strictly gill parasites and suggests three important insights: microhabitat specialisation may be more common than recognised; previous surveys may have missed nasal fossa infections; and competitive release may allow niche expansion.

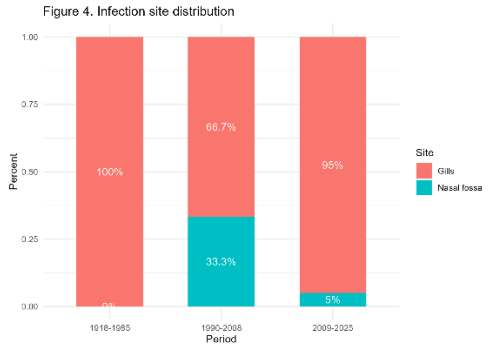

Figure 5. Infection site distribution in *Ergasilus* research. Old trends (1918–1985): 100% gill infection. New trends (1990–2008): 67% gill infection, 33% nasal fossa infection (*E. rhinos*) [4]. Current trends (2009–2025): 95% gill infection, 5% nasal fossa infection (additional species)

Host specificity: generalist or cryptic species

Three species recorded from multiple host families challenge the traditional paradigm of strict host specificity. *Ergasilus clupeidarum* is recorded from four host species across three families (Alosidae and Dorosomatidae), (Fig. 2) making it either a broad generalist or a cryptic species complex. *Ergasilus rhinos* [4] is recorded from three host species within a single family (Centrarchidae), making it a nasal fossa specialist. *Ergasilus uniseriatus* [8] is recorded from two host species across two families (Gobiidae and Belonidae), demonstrating cross-family infection. COI barcoding of specimens from each host is urgently needed to distinguish between cryptic species and true generalism.

Generic revision

The transfer of *PseudErgasilus parasiluri* to *Ergasilus* represents the first molecular confirmation of a generic revision within Ergasilidae [4]. This synonymy was first proposed by Kim & Choi [2] based on morphological evidence, and Song *et al.* [4] provided molecular confirmation. This sets a precedent for re-examining other genera, including *ParaErgasilus*, *Thersitina*, and *Acusicola* [3], using combined molecular and morphological evidence.

The non-monophyly challenge

Recent studies (2024–2025) have revealed that the genus *Ergasilus* is non-monophyletic. Integrative analyses using morphological (27 characters) and molecular (18S rDNA) data from 31 species confirmed polyphyly [4], indicating that the current morphological diagnosis does not reflect evolutionary history. The analysis suggests that at least five new genera may need to be erected, yet no single morphological feature combination robustly supports them. This represents a major taxonomic challenge for future research.

Priority research directions

Based on the persistent gaps identified, ten priority research directions are recommended for 2025–2035. At the global level, sequencing COI for all nominal species is the highest priority, as only approximately 10% currently have barcodes. Providing GPS coordinates for all type localities is the second highest priority, as none currently have coordinates. Completing mitogenomes for 20 or more species is needed, as only 10+ are currently available [4]. Resolving non-monophyly with phylogenomics is essential, as at least five new genera appear to be needed. Examining nasal fossae in all surveys is recommended, as niche expansion has been discovered [4]. Developing eDNA assays would benefit aquaculture monitoring [2]. Testing host specificity experimentally would help resolve whether putative generalists represent true generalism or cryptic species complexes [10].

Regionally, first surveys for *Ergasilus* in Australasia and Oceania are critically needed due to complete absence of records. Intensive sampling of cichlid and catfish hosts in the Neotropical region is a high priority, as Brazil has 76 known species but very few with genetic data [1]. Surveying the African Great Lakes (Tanganyika, Malawi, Victoria) in the Afrotropic region is a high priority due to expected high endemism.

Conclusion

Major findings

This analysis of 90 research records (1918–2025) reveals the following major findings summarized in (Table 1).

Table 1. Major findings of the 90-record analysis (1918–2025)

S. No.	Finding	Old Trends (1918–1985)	New/Current Trends (1990–2025)
1	Molecular revolution	0% DNA data	| 52.2% of records contain DNA data [5, 7]
2	Biogeographic expansion	3 regions represented	6 regions represented [2, 4, 8, 6, 12]
3	Improved taxonomy	Male description: 7.4%	Male description: 66.7% [4, 8]
4	Ecological discovery	No nasal fossa infections	Nasal fossa infection documented [4]
5	Host range expansion	Single host per species	Three species from multiple hosts [2, 12]
6	Generic revision	No generic revisions	First molecular confirmation [5, 12]
7	Non-monophyly	Not recognised	Major taxonomic revision needed [4]

Persistent gaps requiring urgent attention

Several critical gaps persist across all three eras of *Ergasilus* research. GPS coordinates for type localities remain completely absent (0%), representing a critical deficiency for modern taxonomy. COI barcodes are available for only approximately 10% of described species, which is a critical gap for species identification. Australasia and Oceania remains completely unsampled (0 records), representing a critical gap in global coverage.

The Neotropical region, despite contributing 22% of current records, has 76+ known species with very few having genetic data [13], making this a high-priority gap. The Afrotropic region contributes only 11% of current records despite high expected

endemism, representing a high-priority gap. Ecological data remain largely absent (medium priority). Population genetics studies remain completely absent (medium priority).

Authors' contributions

Conceived and designed the experiments: A Batool, Performed the experiments: A Batool, Analyzed the data: A Batool, Contributed materials/ analysis/ tools: A Batool, Wrote the paper: Batool.

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