MUNI SCI Department of Botany and Zoology

Diversity and phylogeny of crustacean ectoparasites (Crustacea: Copepoda) of freshwater fishes of the Old World



Doctoral thesis

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Supervisor: Mgr. Mária Seifertová, Ph.D.

Brno, 2026

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Diverzita a fylogeneze parazitických korýšů třídy Copepoda sladkovodních ryb Starého světa



Dizertační práce

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ABSTRACT

Freshwater parasitic copepods represent an important component of global aquatic biodiversity. This dissertation investigates the diversity, taxonomy, phylogeny and biogeography of parasitic copepods of freshwater fishes, with particular emphasis on the cyclopoid families Ergasilidae and Lernaeidae and a primary focus on Old World regions of Africa, the Mediterranean and the Middle East.

The thesis combines original faunistic surveys, integrative taxonomic analyses based on morphology and molecular data, and a global synthesis of published records. Surveys of Lake Tanganyika uncovered a richer ergasilid fauna than previously recognised, including three new species of *Ergasilus* von Nordmann, 1832 and the first molecular data for African representatives of the genus. Newly described species of *Dermoergasilus* Ho & Do, 1982 from Madagascar and the Mesopotamian basin further demonstrate the persistence of undescribed lineages in isolated island systems and major river drainages of the Old World.

A broad survey of the Mediterranean and Middle East documented numerous new host and country records, described two new species, and generated molecular data for taxa previously lacking sequence information. Phylogenetic analyses consistently supported the polyphyly of *Ergasilus*, highlighted unresolved generic boundaries within both families, and indicated possible cryptic diversity in widely reported taxa.

At the global scale, a comprehensive review of Ergasilidae and Lernaeidae compiled and standardised all available species and genus records worldwide, revealing pronounced geographical biases in sampling effort, a predominance of species known only from original descriptions, and severe limitations in molecular coverage. Several taxonomic adjustments were formalised to stabilise nomenclature and reconcile historical literature with current morphological and phylogenetic evidence.

Overall, the thesis shows that diversity, host associations and distribution patterns of freshwater parasitic copepods remain incompletely resolved, even in comparatively well-studied regions of the Old World and provides a robust baseline for future systematic and biogeographical research on Ergasilidae and Lernaeidae.

ABSTRAKT

Parazitičtí korýši třídy Copepoda představují významnou, avšak dosud nedostatečně prozkoumanou složku globální vodní biodiverzity. Tato dizertační práce se zabývá diverzitou, taxonomií, fylogenezí a biogeografií parazitických klanonožců sladkovodních ryb se zvláštním zaměřením na čeledi Ergasilidae a Lernaeidae a s hlavním důrazem na oblasti Starého světa, zejména Afriku, Středomoří a Blízký východ.

Práce kombinuje vlastní vzorkování, integrativní taxonomické analýzy založené na morfologických a molekulárních datech a globální syntézu publikovaných záznamů. Průzkum jezera Tanganika odhalil výrazně bohatší faunu čeledi Ergasilidae, než bylo dosud známo, včetně popisu tří nových druhů rodu *Ergasilus* von Nordmann, 1832. Rovněž byly získány první molekulární data pro africké zástupce tohoto rodu. Popisy dvou nových druhů rodu *Dermoergasilus* Ho & Do, 1982 z Madagaskaru a Iráku dále potvrzují větší diverzitu v izolovaných ostrovních systémech i ve velkých říčních povodích Starého světa. Rozsáhlý průzkum oblasti Středomoří a Blízkého východu přinesl řadu nových hostitelských a geografických záznamů, popis dalších dvou nových druhů a molekulární data pro taxony, u nichž dosud chyběly. Fylogenetické analýzy opakovaně potvrdily polyfyletický status rodu *Ergasilus*, poukázaly na nevyřešené mezirodové hranice v obou čeledích a naznačily existenci kryptické diverzity u některých široce rozšířených druhů.

Na globální úrovni představuje tato práce první komplexní přehled čeledí Ergasilidae a Lernaeidae, který sjednocuje a standardizuje veškeré dostupné druhové a rodové záznamy. Syntéza odhaluje výraznou geografickou nerovnováhu v intenzitě výzkumu, převahu druhů známých pouze z původních popisů a přetrvávající nedostatek molekulárních dat. Součástí práce je rovněž několik taxonomických úprav, jejichž cílem je stabilizace nomenklatury a sladění historické literatury se současnými morfologickými a fylogenetickými poznatky.

Celkově práce ukazuje, že diverzita, hostitelské vztahy a distribuční vzorce parazitických klanonožců nejsou ještě zcela prozkoumané, a to i v relativně dobře studovaných oblastech Starého světa. Zároveň poskytuje základ pro další systematický a biogeografický výzkum čeledí Ergasilidae a Lernaeidae.

“All we have to decide is what to do with the time that is given us.”
— J.R.R. Tolkien, The Lord of the Rings

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DECLARATION

I hereby declare that this thesis is my own original work, carried out under the supervision of my PhD supervisor. All co-authors of any associated publications are properly acknowledged. All literature sources, data, figures, and other materials used in this thesis are either my own or have been appropriately cited and fully referenced in accordance with academic standards.

Robert Míč

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LIST OF PUBLICATIONS

This dissertation is based on a series of published and unpublished works dealing with the diversity, taxonomy, morphology, biogeography and phylogeny of parasitic copepods of the families Ergasilidae and Lernaeidae. Four articles have been published in peer-reviewed journals, one manuscript is submitted and currently under a review, and one is prepared for submission.

Paper 1

Míč, R., Řehulková, E., & Seifertová, M. (2023). Species of *Ergasilus* von Nordmann, 1832 (Copepoda: Ergasilidae) from cichlid fishes in Lake Tanganyika. *Parasitology*, *150*(7), 579-598. https://doi.org/10.1017/S0031182023000239

Author's contribution: R. M. and M. S. conceived and designed the study. E. Ř. collected parasitological material. R. M. performed morphological characterization and described the species. R. M. and M. S. performed molecular and phylogenetic analyses, and wrote the draft of the manuscript. E. Ř. reviewed descriptions of the species.

My contribution: 70%

Paper 2

Míč, R., Řehulková, E., Šimková, A., Razanabolana, J. R., & Seifertová, M. (2024). New species of *Dermoergasilus* Ho & Do, 1982 (Copepoda: Cyclopoida: Ergasilidae) parasitizing endemic cichlid *Paretroplus polyactis* (Bleeker) in Madagascar. *Parasitology*, *151*(3), 319-336. https://doi.org/10.1017/S0031182024000088

Author's contribution: AŠ, RM and MS conceived and designed the study. EŘ and AŠ collected parasitological material, RM performed morphological characterization and described the species. RM and MS performed molecular and phylogenetic analyses. RM and MS wrote the first draft of the manuscript, EŘ reviewed description of the species.

My contribution: 70%

Paper 3

Míč, R., Hodová, I., Šímková, A., Benovics, M., Šanda, R., Vukić, J., & Seifertová, M. (2025). Diversity and phylogeny of parasitic copepods of freshwater fishes from the Mediterranean and the Middle East. *Parasitology*, 1-28. https://doi.org/10.1017/S0031182025100814

Author's contribution: RM and MS conceived and designed the study. RM, AŠ, MB and MS collected parasitological material, RM performed morphological characterization and

described the species, RŠ and JV collected fishes. RM and MS performed molecular and phylogenetic analyses. IH performed SEM. RM and MS wrote the first draft of the manuscript.

My contribution: 70%

Paper 4 (unpublished manuscript)

Míč, R. & Seifertová, M. (2026). Global diversity of Ergasilidae and Lernaeidae.

Author's contribution: RM and MS conceived and designed the study. RM compiled the dataset and wrote the first draft of the manuscript.

My contribution: 80%

Additional supporting publications

Paper 5 (submitted manuscript in Acta Parasitologica)

Adday, T. K., Ali, A. H., & **Míč R.** (2026). Description of a new species of *Dermoergasilus planilizai* sp. nov. (Copepoda: Ergasilidae) from abu mullet *Planiliza abu* (Heckel) gills at the Al-Gharraf River, Southern Iraq.

Author's contribution: TA and AA conceived and designed the study and collected parasitological material. TA and RM performed morphological characterization and described the species. TA, AA wrote the first draft of the manuscript. RM revised the manuscript.

My contribution: 20%

Paper 6

Kvach, Y., Tkachenko, M. Y., Giannetto, D., **Míč, R.**, Bartáková, V., Ağdamar, S., Saç, G., Özuluğ, M., Tarkan, A. S., & Ondračková, M. (2024). Low Genetic and Parasite Diversity of Invasive Pumpkinseed Lepomis gibbosus (Centrarchidae) Expanding in Türkiye. Diversity, 16(5), 272. https://doi.org/10.3390/d16050272

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My contribution: 10%

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1 INTRODUCTION

Parasitic copepods represent one of the most diverse and ecologically significant groups of crustacean parasites of fishes. They include some of the most widespread and economically important taxa, responsible for gill pathology, tissue damage, secondary infections, and reduced host fitness in both wild and cultured fish populations (Boxshall & Hayes, 2019).

Despite their importance, the diversity, taxonomy, and evolutionary relationships of parasitic copepods remain incompletely understood. Many species are known only from original descriptions, often based on limited material and lacking comparative context. Generic boundaries are frequently unstable, and several widely used genera have been shown to be non-monophyletic (Amado *et al*., 1995; Ho, 1998; Boxshall & Halsey, 2004). Molecular data remain available for only a small fraction of described species, severely limiting phylogenetic conclusions and hindering robust taxonomic revision (Narciso *et al*., 2025; Bernot *et al*., 2025).

Geographic biases further constrain current understanding of parasitic copepod diversity. Large regions of the Old World, including Africa, the Mediterranean basin, and the Middle East, remain unevenly sampled despite hosting highly diverse fish faunas. Historical records from these regions are fragmented across regional literature, museum collections, and unpublished datasets. As a result, patterns of host specificity, biogeographical structure, and parasite dispersal remain poorly resolved.

This dissertation addresses these gaps through a combination of original field sampling, detailed morphological study, targeted molecular analyses, and a critical synthesis of published records. The work centres on the cyclopoid families Ergasilidae Burmeister, 1835 and Lernaeidae Cobbold, 1879 parasitising freshwater fishes, with new material interpreted against a global comparative background. By integrating regional surveys with historical taxonomy and the limited molecular data currently available, the study refines species boundaries, evaluates phylogenetic relationships. This integrative approach clarifies patterns of host use and biogeographical structure within two major lineages of mainly freshwater parasitic copepods.

2 RESEARCH GOALS

The present dissertation aims to investigate the diversity, phylogeny, and host–parasite associations of parasitic copepods, with emphasis on the families Ergasilidae and Lernaeidae infecting freshwater fishes of the Old World. The specific objectives are:

1) To analyse the diversity of parasitic copepods, with particular emphasis on Ergasilidae and Lernaeidae infecting freshwater fishes across selected Old World regions, using morphological examination and molecular characterisation.

2) To reconstruct phylogenetic relationships within these families at multiple taxonomic levels and to clarify generic and species-level limits in the light of both historical and newly obtained data.

3) To evaluate host–parasite associations, with emphasis on host specificity, host range structure, and biogeographical patterns, while placing Old World records into a global context by integrating literature and database records from outside the primary sampling area.

3 LITERATURE REVIEW

3.1 Copepoda: Diversity, Ecology and Parasitism

Copepods are among the most successful metazoans on Earth. Their dominance in marine plankton places them among the most abundant animals globally (Reid & Williamson, 2010). The group currently includes approximately 14,861 described morphospecies, with the highest diversity in marine environments and an estimated 3,262 species recorded from freshwater. Freshwater copepods inhabit a broad range of environments, including ancient lakes, glacial lakes, subterranean waters, hot springs, hypersaline basins, phytotelmata, and semi-terrestrial microhabitats such as wet mosses and forest litter (Martens & Schön, 1999; Galassi *et al*., 2009; Fiers & Jocqué, 2013; Jocqué *et al*., 2013; World of Copepods, accessed 2025). The origin of the group is marine and Huys & Boxshall (1991) hypothesised that all copepod orders recognised at that time originated within the marine hyperbenthic realm. Subsequent biogeographical and phylogenetic analyses identified at least 22 independent colonisations of freshwater across copepod phylogeny (Boxshall & Jaume, 2000). In addition, several marine and estuarine taxa have entered freshwater through their inherent euryhalinity and tolerance of salinity fluctuations (Lee, 1999).

While most freshwater copepods are free-living, parasitism has evolved repeatedly and independently within the group. Approximately 335 freshwater species are parasitic, occurring primarily on fishes but also on molluscs (Boxshall & O'Reilly, 2015). Copepods also occur as commensal epibionts on freshwater invertebrates, including crayfishes, hydromedusae, and sponges (Boxshall & Huys, 1994; Bandera *et al*., 2005; Browne & Kingsford, 2005; Boxshall & Defaye, 2008; Ohtsuka & Ha, 2020). Fish-parasitic copepods comprise a major radiation of parasitic Crustacea, with 1,600–1,800 described species, distributed among Siphonostomatoida (~75%), Poecilostomatoida (~20%), and Cyclopoida (~5%) (Kabata, 1984; Humes, 1994).

Five copepod orders occur in freshwater: Calanoida, Harpacticoida, Cyclopoida, Gelyelloida, and Siphonostomatoida (Boxshall & Halsey, 2004). These groups exhibit a wide range of trophic and ecological strategies, including microphagous suspension feeding, predation, commensalism, and parasitism. The Cyclopidae represent the largest freshwater family, comprising more than 800 species (Dussart & Defaye, 2006). Several freshwater

lineages within Cyclopoida exhibit extensive morphological and ecological specialisation associated with parasitism. Among these, the Ergasilidae and Lernaeidae represent the principal freshwater parasitic families and form the focus of the present dissertation.

3.2 Morphology of copepods and their adaptations for parasitism

Copepods are remarkably diverse in body shape, but in general they share physical features that unite them as a group. Parasitic copepods often differ from free-living forms in exhibiting varying degrees of body modification, frequently associated with the loss or reduction of appendages and segmentation (Kabata, 1979; Holmes & Price, 1986). The extent of these modifications differs widely among taxa, ranging from slight reductions of rami or setation to pronounced changes in body form. In some parasitic lineages, adults become elongate or vermiform, whereas others develop compact or rounded bodies (Kabata, 1979; Poulin, 2007).

Generally, copepods exhibit two principal body plans corresponding to their taxonomic superorders. In gymnoplean copepods, the prosome–urosome articulation occurs between the fifth pedigerous and genital somites. In podoplean copepods, which include all parasitic taxa, the prosome–urosome articulation occurs between the fourth and fifth pedigerous somites (Fig. 1). The prosome is five-segmented, comprising the cephalosome and four free pedigerous somites. The urosome is primitively six-segmented in both sexes, consisting of the fifth pedigerous somite, the genital somite, and four abdominal somites. In adult females, the genital and first abdominal somites fuse to form a genital double-somite, whereas in males these segments remain separate. The terminal abdominal somite bears the anus and paired caudal rami (Huys & Boxshall, 1991). The cephalosome comprises the five-segmented cephalon and the first thoracic somite, which bears the maxilliped. The cephalon carries five pairs of appendages: antennules, antennae, mandibles, maxillules, and maxillae. Antennules are uniaxial limbs with up to 27 segments, each bearing setae and aesthetascs. In many podoplean taxa, including parasitic copepods, several articulations are suppressed, resulting in a reduced number of expressed segments (Boxshall & Huys, 1998). Antennae are primitively biramous; however, in most parasitic groups the exopod is reduced or lost, and the endopod forms the primary axis, often terminating in hooks or claws used for attachment on the host (Kabata, 1979; Boxshall & Hayes, 2019).

The mouthparts consist of mandibles, maxillules, maxillae, and maxillipeds. Mandibles possess a coxal gnathobase proximally and a distal palp that is primitively biramous but may be reduced or lost in parasitic taxa. Mandible form and position relative to the labrum and paragnaths vary among copepod orders and are important diagnostic characters (Huys & Boxshall, 1991). Maxillules are primitively biramous, though parasitic forms typically lose the exopod and exhibit overall limb reduction. The maxilla is uniramous, with a protopodal region bearing endites in primitive forms and a distal endopod that in many parasitic taxa bears claws or hooks used for feeding or attachment. In highly transformed parasitic lineages, cephalosomal appendages may be markedly reduced (Huys & Boxshall, 1991). Some parasitic copepods also possess specialised mouthparts such as stylets or hooks that facilitate penetration of host tissues (Kabata, 1979).

Copepods primitively possess six pairs of thoracic appendages (pereopods, P1–P6), which differ in structure and function. The first four pairs of swimming legs (P1–P4) are biramous and primitively three-segmented in each ramus. These limbs articulate with a broad protopod that includes a coxa and basis, and the rami move synchronously due to their articulation via an intercoxal sclerite, a diagnostic copepod feature present from the earliest copepodid stages (Huys & Boxshall, 1991). The fifth pair of legs (P5) occur on the first urosomite and is typically reduced, commonly through loss or reduction of the endopod. The sixth pair of legs (P6) is not involved in locomotion and is associated with the genital segment, strongly reduced in parasitic copepods and typically expressed as a small lobe or opercular element forming part of the genital opening (Kabata, 1979; Huys & Boxshall, 1991). The specific armature patterns of spines, setae, and setal formulae on the swimming legs are important taxonomic characters at all hierarchical levels (Kabata, 1979; Boxshall & Hayes, 2019). In many parasitic copepods, the thoracic legs are reduced or modified in accordance with decreased locomotory requirements (Kabata, 1979).

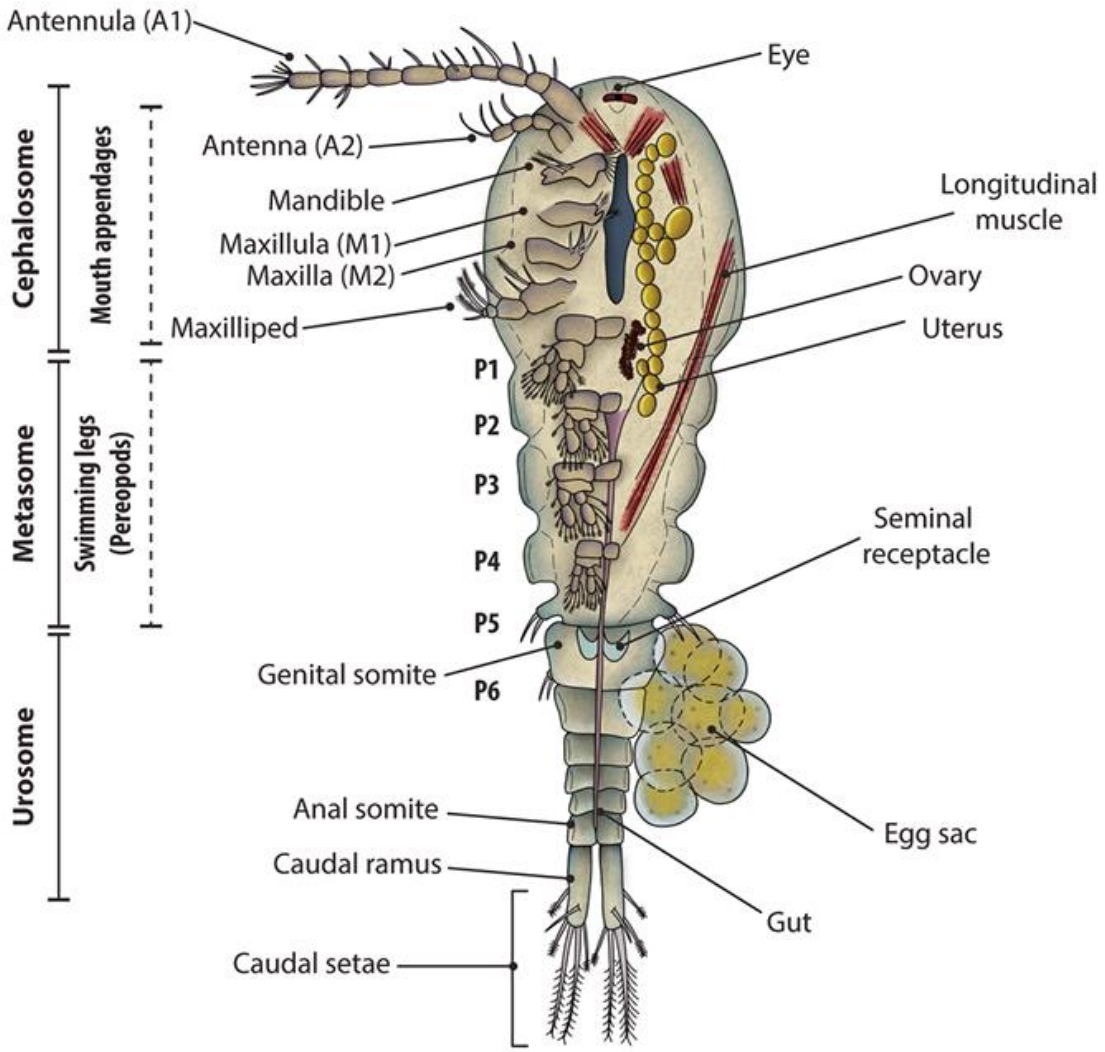


Fig. 1: Generalised morphology of a copepod, ventral view with external appendages shown on the left side, internal organs visible on the right side. Abbreviations: A1: Antennula 1, A2: Antenna 2, M1: Maxillula 1, M2: Maxilla 2, P1–6: pereopods (reproduced from Hadfield *et al*., 2025).

3.3 Life cycle of parasitic copepods

The life cycle of parasitic copepods is characterised by a combination of free-living larval development and host-associated parasitic stages (Fig. 2, 3). In most lineages parasitizing fishes, eggs are carried in paired external sacs or strings and are released into the water shortly before hatching. This strategy enhances larval survival in flowing or turbulent waters (Kabata, 1979; Izawa, 1987).

Hatching produces a nauplius larva bearing an unsegmented body and three functional pairs of appendages, namely antennules, antennae and mandibles. Up to six naupliar stages

may occur, all of which are free-living. Nauplii may be planktotrophic, but in many parasitic lineages the naupliar stages are lecithotrophic. They exhibit reduced setation on the three pairs of appendages, and lack a functional naupliar feeding process on the antennal coxae. In some parasitic taxa, naupliar stages are reduced in number or absent altogether (Kabata, 1979; Izawa, 1987; Ismail *et al*., 2013; Boxshall & Hayes, 2019).

The final nauplius moults into the first copepodid stage, which includes the transition to a segmented body plan with the full complement of cephalic appendages and the first thoracic swimming legs. Up to five copepodid stages occur, with additional thoracic somites added at each moult (Kabata, 1979). In most parasitic copepods, the first copepodid stage is free-living, whereas subsequent copepodid stages may be infective, depending on the taxon (Boxshall & Halsey, 2004). The fifth copepodid stage moults into the adult, with sexual differentiation apparent at this stage. Female copepodids become sexually receptive at the final moult (Boxshall & Hayes, 2019).

Mating generally occurs soon after the final moult. Males locate females using chemosensory aesthetascs on the antennules that detect female-produced pheromones (Katona, 1973; Griffiths & Frost, 1976; Uchima & Murano, 1988). In some taxa, males engage in precopulatory mate guarding, grasping pre-adult females until they moult into the adult stage (Boxshall, 1990). During copulation, one or more spermatophores are transferred to the female genital region, where sperm are stored prior to fertilisation. Males typically die shortly after mating (Boxshall & Hayes, 2019).

Among fish-parasitic cyclopoids, post-mating development varies markedly. In some groups, adult females retain a broadly cyclopiform body plan and remain ectoparasitic throughout life. These forms attach to external host surfaces, such as the gills, skin or fins, using prehensile appendages modified for clasping. In other taxa, fertilised females undergo profound post-mating metamorphosis. They become permanently embedded within host tissues, develop specialised anchoring structures and progressively lose external segmentation (Hadfield *et al*., 2025). These contrasting trajectories are exemplified by the mainly ectoparasitic strategy of ergasilid females and the highly transformed, tissue-embedded females of lernaeids.

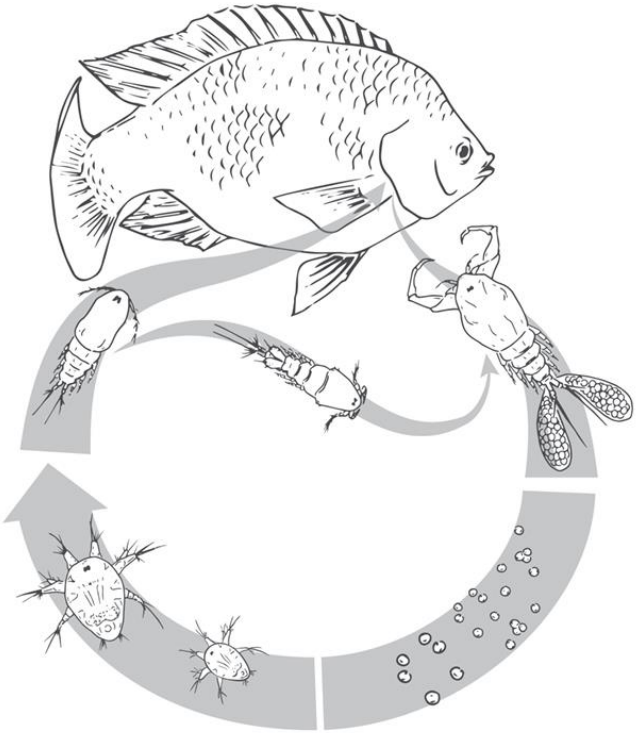


Fig. 2: Life cycle of *Ergasilus* sp. (Copepoda: Cyclopoida) showing free-living naupliar and copepodid stages and the parasitic adult female attached to the fish host. Males remain free-living throughout the life cycle (reproduced from Smit *et al*., 2019).

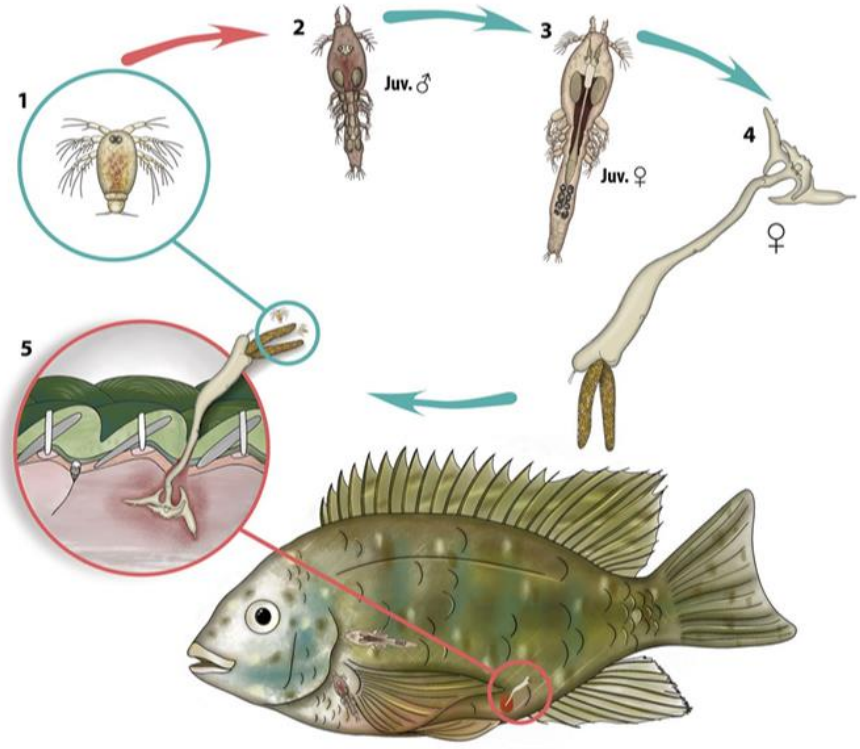


Fig. 3: Typical life cycle of *Lernaea* sp. (Copepoda: Cyclopoida) parasitising freshwater fish. Naupliar larvae (1) hatch from egg sacs and develop through free-living naupliar and copepodid stages (2). Sex is determined at the final copepodid stage, after which mating occurs. The fertilised female undergoes post-mating metamorphosis (3–4) and becomes permanently embedded in host tissues by a branched holdfast (5), while males die shortly after copulation (reproduced from Hadfield *et al*., 2025).

3.4 Taxonomy of copepods and their parasitic lineages

The higher-level classification of Copepoda has been revised repeatedly, and several deep phylogenetic relationships within the group remain not fully resolved (Bernot *et al*., 2025). Current systematics recognises two infraclasses, Progymnoplea Lang, 1948 and Neocopepoda Huys & Boxshall, 1991, the latter containing the vast majority of diversity and all parasitic taxa. Neocopepoda is divided into the superorders Gymnoplea Giesbrecht, 1882 and Podoplea Giesbrecht, 1882. Gymnoplea contains the single order Calanoida Sars, 1903, a group composed entirely of free-living planktonic copepods. Podoplea comprises eight orders, including the major lineages that have evolved parasitism. Parasitic representatives are known from Canuelloida Khodami, Vaun MacArthur, Blanco-Bercial & Martinez Arbizu, 2017 (often cited as Polyarthra Lang, 1944), Cyclopoida Burmeister, 1834 (including Poecilostomatoida), Harpacticoida Sars, 1903, Monstrilloida Sars, 1901, and Siphonostomatoida Burmeister, 1835. The remaining podoplean orders, Gelyelloida Huys, 1988, Misophrioida Gurney, 1933 and Mormonilloida Boxshall, 1979, are free-living (Huys & Boxshall, 1991; Boxshall & Defaye, 2008).

Fish parasitism occurs within three podoplean orders: Cyclopoida, Harpacticoida and Siphonostomatoida. Recent phylogenetic syntheses based on combined morphological and molecular evidence support the monophyly of several major podoplean lineages, although the placement of some taxa remains unresolved, most notably Gelyelloida, for which molecular data are still unavailable (Bass *et al*., 2021) (Fig. 4).

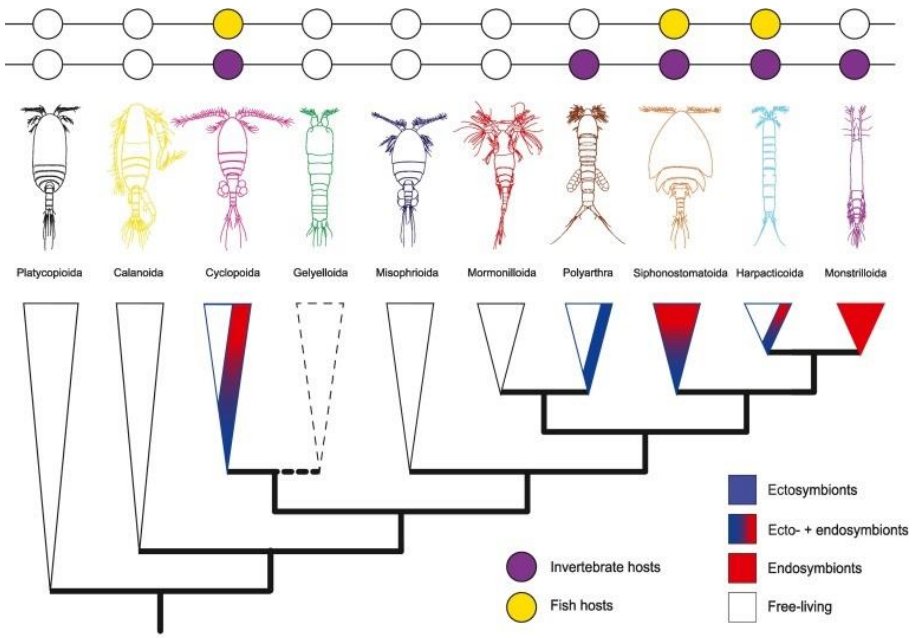


Fig. 4: Phylogenetic hypothesis of interordinal relationships within the Copepoda, the position of Gelyelloida (no molecular data available) is intercalated, based on morphological data. The colour shading in the phylogram (red to blue) indicates relative numbers of species in these copepod clades that are either free-living (white), endosymbiotic (red), or ectosymbiotic (blue). The circles on top of the graph indicate if copepods parasitize invertebrate (purple) or fish (yellow) hosts (reproduced from Bass *et al*., 2021).

3.4.1 Harpacticoida Sars, 1903

The order Harpacticoida are predominantly benthic free-living copepods, although several symbiotic and parasitic lineages are recognised. Parasitic harpacticoids are comparatively few and occur on both vertebrate and invertebrate hosts. Species of *Balaenophilus* Aurivillius, 1879 inhabit the external surfaces of marine turtles, baleen whales, and manatees, where they occur as epibionts and have been regarded as facultative parasites. Other parasitic harpacticoids, particularly within the family Tisbidae, occur on cephalopods, especially octopuses, where they inhabit gill chambers or the external body surface (Humes & Voight, 1997; Avdeev, 2010).

Harpacticoids are distinguished from other copepods by several diagnostic morphological features. The antennules are typically short and unsegmented or only weakly segmented. The antennae are biramous, with the exopod frequently reduced. The major prosome–urosome articulation is located between the fourth and fifth pedigerous somites. Thoracic legs P1–P4 are generally robust and adapted to benthic locomotion, reflecting their predominantly interstitial or substratum-associated lifestyle (Reid & Williamson, 2010). Parasitic lineages

retain the general harpacticoid body plan but exhibit varying degrees of appendage reduction or setal modification.

3.4.2 Siphonostomatoida Burmeister, 1835

The order Siphonostomatoida comprises the largest radiation of parasitic copepods, representing approximately 75% of known fish-parasitic species. Members of this order are primarily marine, although a small number of taxa occur in freshwater. Siphonostomatoids are characterised by the presence of a cephalothorax with a siphon-like oral cone enclosing stylet-like mandibles, this structure is considered a principal adaptation to feeding on host tissues (Kabata, 1979). Most families attach to their hosts by a chitinous plug, the bula, which is inserted into the host epidermis and secured by modified maxillary processes (Boxshall & Halsey, 2004).

Host diversity within the order is extensive, including agnathans, elasmobranchs, holocephalans, and teleosts (Boxshall & Hayes, 2019). Several families parasitise invertebrates; for example, Nicothoidae are obligate ectosymbionts of crustaceans (Boxshall & Ohtsuka, 2001; Boxshall & Halsey, 2004). The family Caligidae, commonly referred to as sea lice, contains over 400 species, nearly all marine, except *Caligus lacustris* Steenstrup & Lütken, 1861, which occurs in freshwater and brackish environments, including the Black Sea. Caligid copepods are of considerable interest due to their role in the parasitism of commercially important salmonid fishes.

Within Lernaeopodidae, the Salmincola clade comprises 38 species distributed across seven genera, all parasitising freshwater or anadromous fishes (Kabata, 1979). Adult females of several families develop strongly transformed bodies, often enlarged, fleshy, and with reduced or obscured external segmentation, whereas males typically retain a more cyclopiform morphology. In taxa such as the Lernaeopodidae and Pennellidae, females produce large uniseriate or multiseriate egg sacs, in some cases forming extremely elongate egg strings containing numerous embryos (Kabata, 1979; Boxshall & Halsey, 2004).

3.4.3 Cyclopoida Burmeister, 1834

The order Cyclopoida includes free-living forms, commensals and a large number of parasites. The family Cyclopidae represents the most species-rich freshwater copepod family. Symbiotic and parasitic cyclopoids exhibit exceptional host diversity. Over 2700 species are

associated with invertebrate hosts, including bivalve and gastropod molluscs, cephalopods, chitons, scaphopods, polychaetes, echinoderms, hemichordates, enteropneusts, phoronids, nemerteans, turbellarians, and crustaceans (Ho & Perkins, 1977; Ho, 1984; Ho & Thatcher, 1989; Franz & Bullock, 1990; Ohtsuka *et al*., 2010; Boxshall & O'Reilly, 2015; Kim *et al*., 2016; Boxshall & Hayes, 2019; Pascual *et al*., 2019; Cheng *et al*., 2023).

More than 950 cyclopoid species parasitise fishes. Most are ectoparasites of the gills or body surface. The family Philichthyidae comprises species that inhabit the lateral line canals of marine fishes. Within freshwater systems, the family Ergasilidae contains numerous gill parasites, including the genus *Urogasilus* Rosim, Boxshall & Ceccarelli, 2013, whose species reside in the urinary bladder of certain fishes. The family Ozmanidae includes two endoparasitic species inhabiting freshwater gastropod hosts in South America (Grabda & Linkowski, 1978; Piasecki et al., 2004; Madanabeitia *et al*., 2013; Rosim *et al*., 2013).

The former order Poecilostomatoida is now treated within Cyclopoida sensu lato on the basis of morphological and molecular evidence. Most poecilostomatoid copepods are ectoparasitic on invertebrates or fishes, although certain taxa are endoparasitic (Boxshall & Hayes, 2019). Cyclopoids display substantial morphological variability associated with parasitism, particularly in antennal and maxillipedal structures, which are frequently modified for attachment.

Within Cyclopoida, parasitic species are distributed worldwide. Among these, the families Ergasilidae and Lernaeidae occur primarily on freshwater fishes across all major zoogeographical regions and represent the dominant parasitic cyclopoid lineages globally (Boxshall & Defaye, 2008). Both families are also widely distributed in the Old World, where they form a substantial component of the freshwater parasitic copepod fauna. These families are therefore reviewed in detail below.

3.5 Ergasilidae von Nordmann, 1832

The family Ergasilidae is one of the major parasitic lineages within the poecilostome Cyclopoida and currently includes 284 valid species in 29 valid genera, with *Anklobrachius* Thatcher, 1999 regarded as *genus inquirendum* (Boxshall & Halsey, 2004) (Fig. 5, 6, 7). Adult female ergasilids are typically parasitic on actinopterygian fishes, whereas all developmental stages from nauplius through to adult are free-living components of planktonic communities

(Kabata, 1979; Izawa, 1987; Boxshall & Defaye, 2008). Males are free-living throughout their lives. After mating, fertilised females attach to hosts for the parasitic phase. At certain seasons, ergasilid developmental stages may be locally abundant or dominant in freshwater, estuarine, or coastal lagoonal plankton (Boxshall & Defaye, 2008). Although the great majority of species utilise fishes as hosts, a genus *Teredophilus* Rancurel, 1954 and *Paraergasilus rylovi* Markevich, 1937, are parasites of freshwater bivalves (Markevich, 1937; Rancurel, 1954).

Most species of Ergasilidae are freshwater, but some occur in brackish and marine environments, with 19 species reported from marine habitats (Tang & Kalman, 2008; van der Spuy *et al*., 2025). They can cause haemorrhaging and severe gill damage at the location of attachment or secondary infections at the site of the attachment (Piasecki *et al*., 2004). High intensity of infection can lead to weak swimming, gulping at the surface, and death (Lester & Hayward, 2006). Ergasilids are also implicated as a possible disease vector or as a potential reservoir host for viruses (Nigrelli, 1950; Jones & Hine, 1983; Overstreet *et al*., 2009).

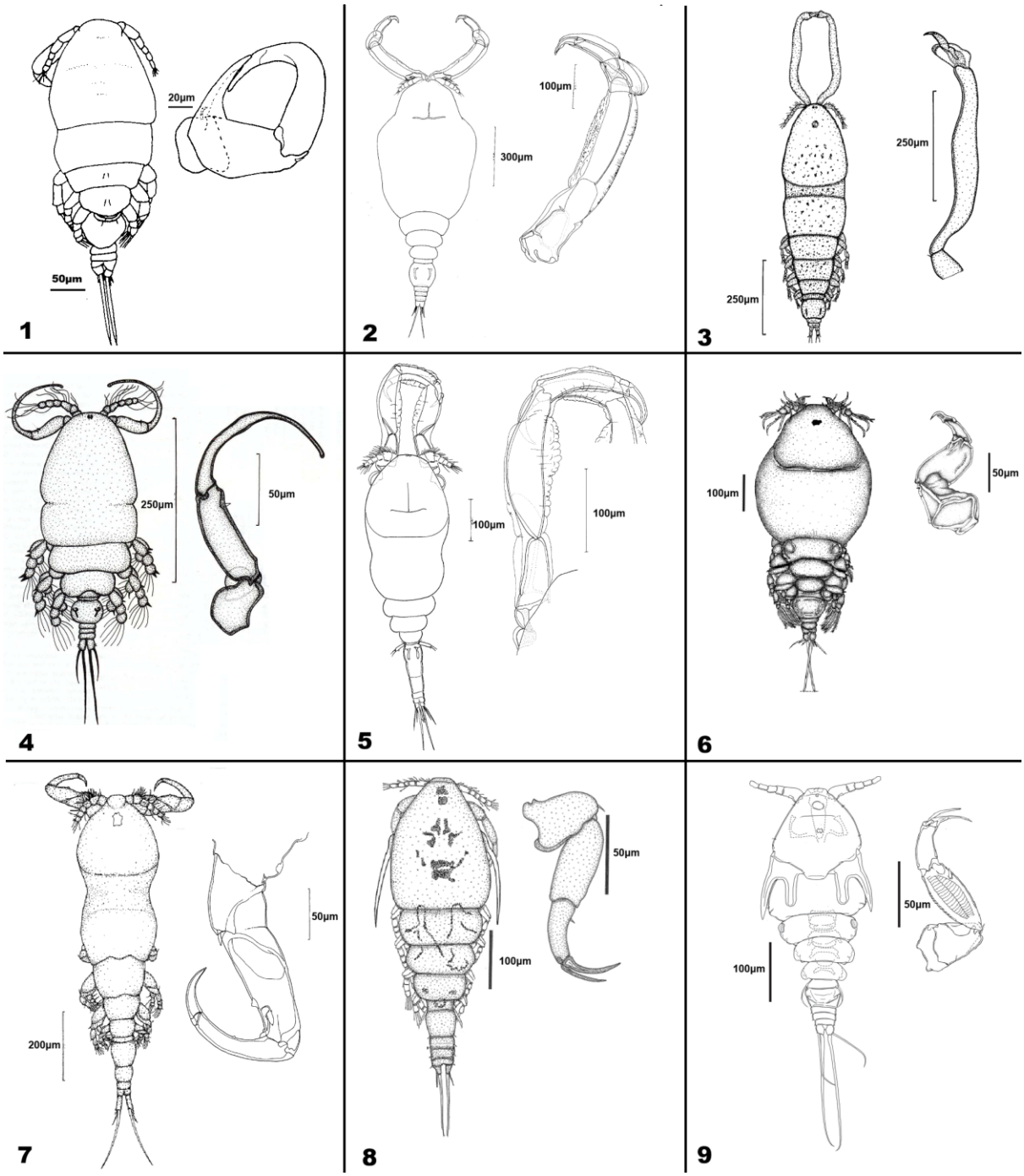


Fig. 5: Adult females of representative species from the genera of Ergasilidae, showing general habitus and the antenna. (1) *Abergasilus* Hewitt, 1978; (2) *Acusicola* Cressey, 1970; (3) *Amplexibranchius* Thatcher & Paredes, 1985; (4) *Brasergasilus* Thatcher & Boeger, 1983; (5) *Dermoergasilus* Ho & Do, 1982; (6) *Duoergasilus* Narciso, Brandão, Perbiche-Neves & da Silva, 2019; (7) *Ergasilus* von Nordmann, 1832; (8) *Gamidactylus* Thatcher & Boeger, 1984; (9) *Gamispatulus* Thatcher & Boeger, 1984. Adapted from Hewitt (1978); Thatcher & Boeger (1983, 1984); Thatcher & Paredes (1985); Alston *et al*. (1993); El-Rashidy & Boxshall (1999, 2001b); Thatcher *et al*. (2008); Narciso *et al*. (2019).

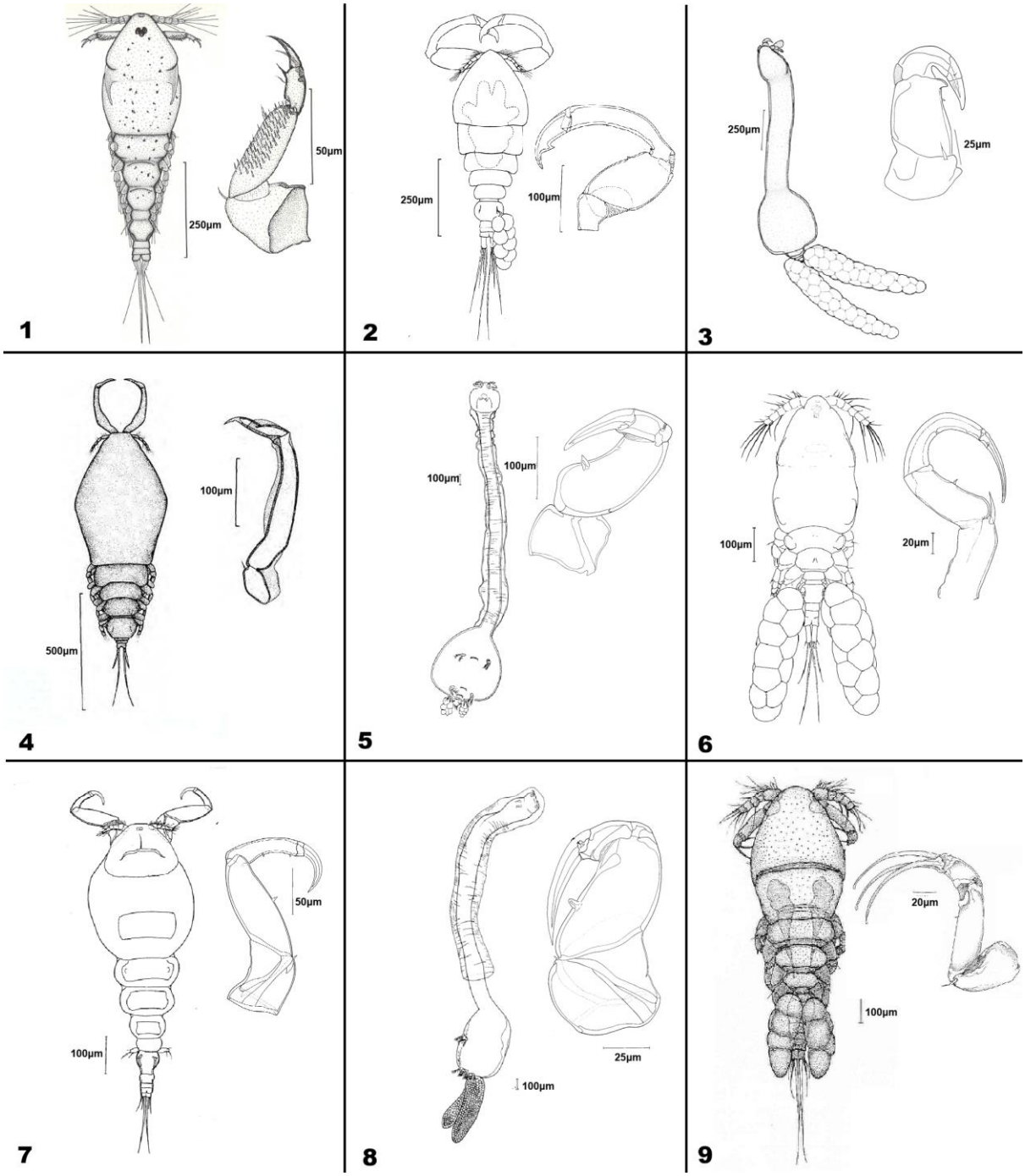


Fig. 6: Adult females of representative species from the genera of Ergasilidae, showing general habitus and the antenna. (1) *Gamispinus* Thatcher & Boeger, 1984; (2) *Gauchergasilus* Montú & Boxshall, 2002; (3) *Majalincola* Tang & Kalman, 2008; (4) *Miracetyma* Malta, 1993; (5) *Mugilicola* Tripathi, 1960; (6) *Neoergasilus* Yin, 1956; (7) *Nipergasilus* Yamaguti, 1939; (8) *Paeonodes* Wilson, 1944; (9) *Paraergasilus* Markevich, 1937. Adapted from Do, (1982); Thatcher & Boeger (1984); Malta (1993); El-Rashidy & Boxshall (2000, 2001a); Montú & Boxshall (2002); Kim & Choi (2003); Tang & Kalman (2008).

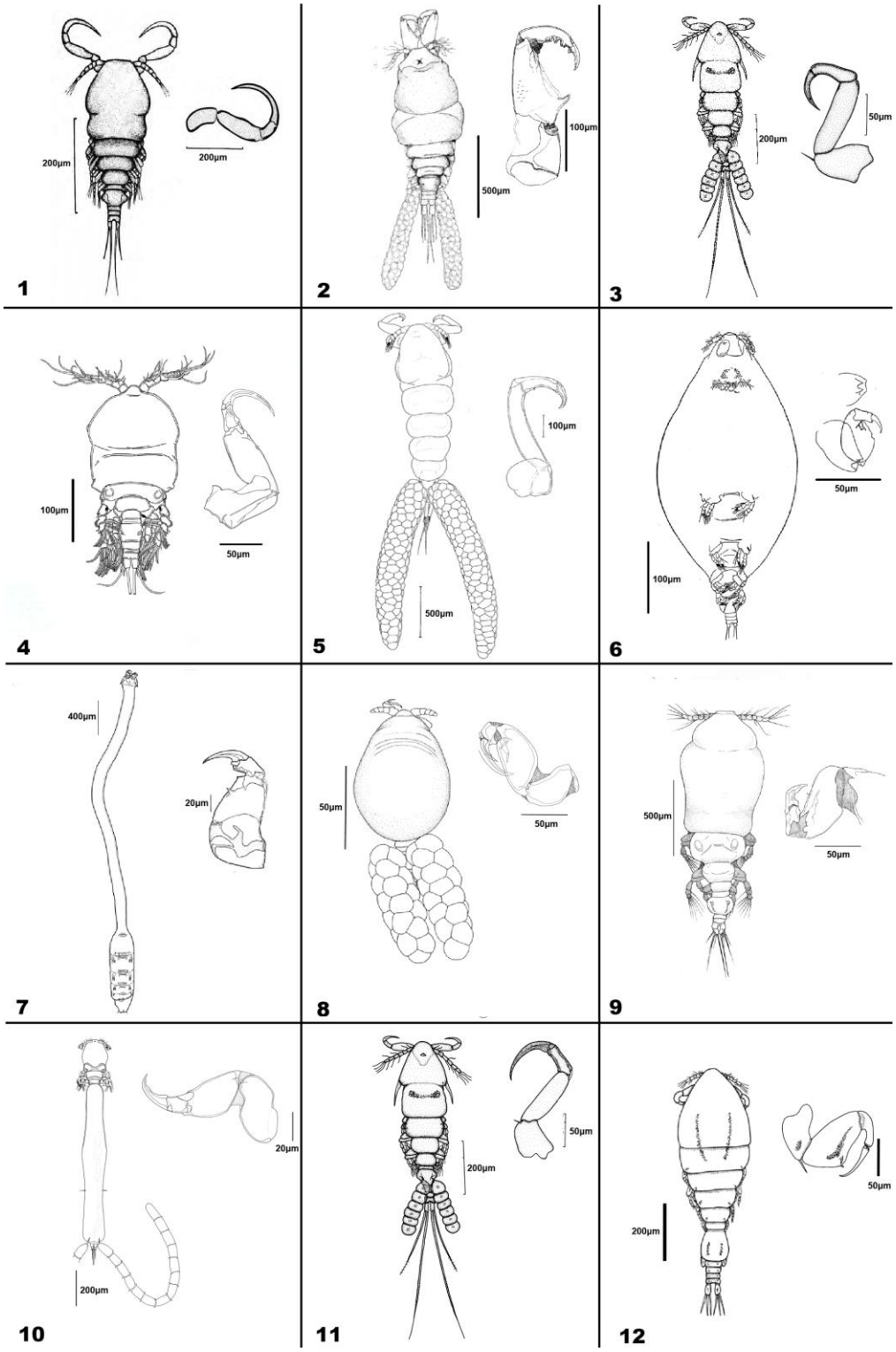


Fig. 7: Adult females of representative species from the genera of Ergasilidae, showing general habitus and the antenna. (1) *Pindapixara* Malta, 1995; (2) *Prehendorastrus* Boeger & Thatcher, 1990; (3) *Pseudovaigamus* Amado, Ho & Rocha, 1995; (4) *Rhinergasilus* Boeger & Thatcher, 1988; (5) *Sinergasilus* Yin, 1949; (6) *Teredophilus* Rancurel, 1954; (7) *Therodamas* Krøyer, 1863; (8) *Thersitina* Norman, 1905; (9) *Tiddergasilus* Marques & Boeger, 2018; (10) *Urogasilus* Rosim, Boxshall & Ceccarelli, 2013; (11) *Vaigamus* Thatcher & Robertson, 1984; (12) *Anklobrachius* Thatcher, 1999 – *genus inquirendum*. Adapted from Rancurel (1954); Thatcher & Robertson (1984); Boeger & Thatcher (1990); Malta (1995); Thatcher (1999); Kim & Choi (2003); Ohtsuka *et al*. (2004a); Rosim *et al*. (2013); Marques & Boeger (2018); Narciso *et al*. (2020b); Oliveira *et al* (2021).

3.5.1. History and discovery rate of Ergasilidae

Early work on Ergasilidae in the nineteenth century focused mainly on descriptions of species and on attempts to delimit higher taxa among poecilostomatoid copepods. *Ergasilus* was introduced by von Nordmann (1832), but the family was not formalised until Burmeister (1835), who grouped several morphologically disparate genera under the name Ergasilina. This broad concept reflected the limited structural information available and distinguished taxa mainly based on the variation in the oral region. Subsequent authors adopted or modified this view and included many genera that are not regarded as ergasilids today, while Krøyer (1837) provided the first description of a male specimen. Baird (1850) and Dana (1852, 1853) used the family name widely and Ergasilina was placed within Poecilostoma. Claus (1864) demonstrated that *Ergasilus* differed from several genera long associated with it, particularly *Bomolochus* von Nordmann, 1832; *Nicothoë* Audouin & Milne-Edwards, 1825 and *Lichomolgus* Thorell, 1859, which he removed based on morphology. Later treatments accepted or rejected these exclusions with varying levels of caution, and generic lists continued to fluctuate into the late nineteenth century (Heller, 1865). During this long initial phase, the number of valid genera remained low. In addition to *Ergasilus*, only a few other genera now included in the family were described, notably *Therodamas* Krøyer, 1863 and *Thersitina* Norman, 1905, and overall generic diversity increased only slowly (Krøyer, 1863; Norman, 1905).

The first structured internal framework was introduced by Wilson (1911), who subdivided the family using characters of the antennae and maxillipeds. Although his subdivisions were later abandoned, the comparative anatomical approach he employed became the basis for subsequent ergasilid systematics. Early twentieth century authors also reassessed generic limits. Sars (1918) removed *Bomolochus* from Ergasilidae and recognised *Thersitina*, *Ergasilus* and *Ergasiloides* Sars, 1909, the last of which was later synonymised with *Ergasilus*. The period from the 1930s to the 1950s brought an increase in generic richness with the description of *Paraergasilus* Markevich, 1937, *Nipergasilus* Yamaguti, 1939, *Paeonodes* Wilson, 1944, *Sinergasilus* Yin, 1949, *Teredophilus* Rancurel, 1954, *Neoergasilus* Yin, 1956 and *Mugilicola* Tripathi, 1960. These additions mainly resulted from increased sampling in Asia, Eastern Europe and North America (Markevich, 1937; Yamaguti, 1939; Wilson, 1944; Yin, 1949, 1956; Tripathi, 1960).

From the latter half of the twentieth century onwards, intensive study of appendage morphology and increasing exploration of tropical freshwaters produced another wave of generic discovery. Tripathi (1960) proposed Therodamasinae, originally at family rank, for genera with an apparently neck-like cephalothorax, including *Therodamas*, *Paeonodes* and *Mugilicola*. Further work from the 1970s and 1980s documented additional morphological diversity and led to the description of several Neotropical genera (Cressey & Collette, 1970; Thatcher & Boeger, 1983, 1984; Thatcher & Paredes, 1985a). These include *Acusicola* Cressey & Collette, 1970, *Brasergasilus* Thatcher & Boeger, 1983, *Gamidactylus* Thatcher & Boeger, 1984, *Gamispatulus* Thatcher & Boeger, 1984 and *Gamispinus* Thatcher & Boeger, 1984 and *Amplexibranchius* Thatcher & Paredes, 1985. From other regions, *Abergasilus* Hewitt, 1978 was described from Australia and *Dermoergasilus* Ho & Do, 1982 from the Oriental region (Hewitt, 1978; Ho & Do, 1982). Additional genera established during this period include *Prehendorastrus* Boeger & Thatcher, 1990, *Miracetyma* Malta, 1993, *Pindapixara* Malta, 1995 and *Pseudovaigamus* Amado, Ho & Rocha, 1995, all of them from South America (Boeger & Thatcher, 1990; Malta 1993, 1995; Amado *et al*., 1995). This interval produced the steepest increase in the cumulative number of genera and also prompted several subfamilial proposals, including Ergasilinae, Abergasilinae, Therodamasinae and Acusicolinae (Thatcher & Boeger, 1983; Thatcher, 1984). Subsequent analyses showed that the characters used to define these subfamilies did not correspond to monophyletic lineages. Cressey (1972) showed that *Therodamas* displays typical ergasilid morphology and later work synonymised *Amazonicopeus* with *Therodamas*. Boxshall (1986) clarified that the elongate cephalic region in *Mugilicola* and *Paeonodes* differs structurally from that of *Therodamas* but that all three genera belong within Ergasilidae. The cladistic study of Amado *et al.* (1995) incorporated these observations and placed the former Therodamasidae within Ergasilidae. Modern syntheses therefore treat the family as unsplit at subfamily level (Boxshall & Halsey, 2004).

In parallel with this increase in described genera, comparison of type material led to numerous synonymies. El Rashidy & Boxshall (2001a) proposed that *Paeonodes* and *Mugilicola* form a single lineage. *Paeonodes* has priority as the valid genus, but *Mugilicola* has been retained provisionally pending a comprehensive revision (Boxshall & Halsey, 2004). Ohtsuka *et al.* (2004a) showed that *Diergasilus* Do, 1981 is indistinguishable from *Thersitina* and reduced it to synonymy. *Limnoncaea* Kokubo, 1914, originally placed in Oncaeidae, was

found to contain species referable to *Ergasilus* and *Thersitina* (Ohtsuka *et al*., 2004b). Kabata (1992) questioned the validity of *Dermoergasilus*, but descriptions of three new species and a revised identification key provided by El Rashidy & Boxshall (2001b) supported recognition of the genus, this conclusion was also followed by Míč *et al.* (2024). The genus *Byrnesius* Kazachenko, 1991, erected for *Ergasilus spinipes* Byrnes, 1986 by Kazachenko (2001), was regarded as indistinguishable from *Neoergasilus* and treated as its synonym by Boxshall & Halsey (2004). Historical names such as *Macrobrachinus* Hesse, 1871 and *Megabrachinus* Hesse, 1871 were retained as *genera inquirenda* based on their outdated descriptions that does not enable to assess their status (Kabata, 1979; Boxshall & Halsey, 2004).

The early twenty-first century has seen a slower but still positive increase in generic richness (Fig. 8), largely through work in previously undersampled tropical drainages (Montú & Boxshall, 2002; Tang & Kalman, 2008; Rosim *et al*., 2013; Marques & Boeger, 2018; Narciso *et al*., 2019). New genera described during this period include *Gauchergasilus* Montú & Boxshall, 2002, *Majalincola* Tang & Kalman, 2008, *Urogasilus* Rosim, Boxshall & Ceccarelli, 2013, *Tiddergasilus* Marques & Boeger, 2018 and *Duoergasilus* Narciso, Brandão, Perbiche-Neves and da Silva, 2019. All of these are Neotropical in origin, with *Majalincola* representing an Australian contribution.

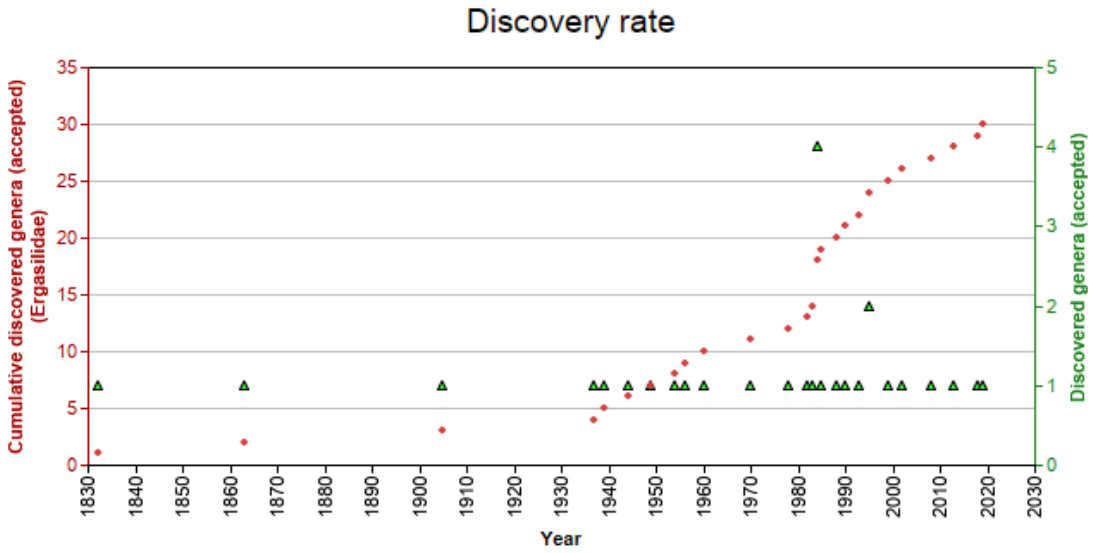


Fig. 8: Cumulative discovery rate of valid genera of Ergasilidae through time, based on data compiled from the World of Copepods database (accessed 2025).

Species-level discovery shows a parallel but more continuous pattern. Nineteenth century contributions produced only a small number of valid species, mostly within *Ergasilus*, and the

cumulative total increased slowly until the early twentieth century. From the 1930s onwards, improved access to freshwater ichthyofaunas in Asia and Eastern Europe produced a moderate rise in species descriptions (e. g. Yamaguti, 1939; Markevich, 1940, 1946; Capart, 1944; Yin, 1949). The most rapid phase of accumulation occurred between the 1960s and the late 1990s (Fig. 9). Systematic surveys in South America, Africa and Southeast Asia revealed extensive uncharted diversity associated with widely distributed and regionally endemic hosts (e. g. Fryer, 1961, 1964, 1965, 1968; Kuang & Qian, 1983, 1985; Thatcher, 1984; Thatcher & Boeger, 1985). During this period several years recorded multiple new species and the slope of the cumulative curve increased more sharply than at any earlier time. The period from the early 2000s to the present shows a lower but still clearly positive rate, with new species originating from Neotropical, Oriental, African and Australasian basins that continue to be incompletely sampled (e. g. El-Rashidy & Boxshall, 2001a,b; Narciso *et al.*, 2019, 2020a,b, 2022; Waicheim *et al*., 2021; Míč *et al*, 2023, 2024, 2025).

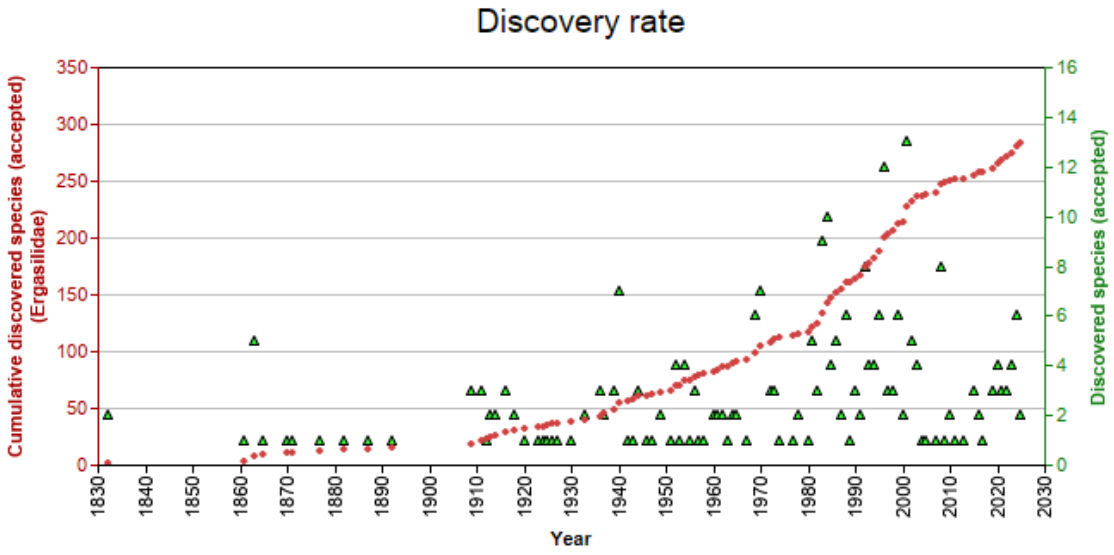


Fig. 9: Cumulative discovery rate of valid species of Ergasilidae through time, based on data compiled from the World of Copepods database (accessed 2025).

3.5.2 Host range and sites of infection in Ergasilidae

The Ergasilidae display a wide range of parasitic strategies but mostly remain associated with freshwater actinopterygian fishes. The richest genus *Ergasilus*, which includes 165 valid species, is almost entirely restricted to teleosts, but rare host switching into elasmobranch lineages has been documented in three species: *Ergasilus myctarothes* Wilson, 1913 from the nasal fossae of *Sphyrna zygaena* off Jamaica (Wilson, 1913); *Ergasilus ogawai* Kabata, 1992

from *Pristis microdon* and *Lates calcarifer* in northern Australia (Kabata, 1992); and *Ergasilus trygonophilus* Domingues & Marques, 2010 from freshwater stingrays of the genus *Potamotrygon* in the Amazon Basin (Domingues & Marques, 2010). *Teredophilus* is the only ergasilid genus parasitic strictly on non-vertebrate hosts, being associated exclusively with brackish-water bivalves and *Paraergasilus rylovi* has been reported from plankton, fishes and also from bivalve molluscs.

Most ergasilids are ectoparasites of the gills, where modified prehensile second antennae secure the adult female to the filaments or arches (Boxshall & Halsey, 2004). Several lineages have independently colonised the nasal cavities, particularly in the Neotropics, where the genera *Brasergasilus*, *Gamidactylus*, *Gamispatulus*, *Gamispinus*, *Rhinergasilus* and *Therodamas* include one or more species specialised for this microhabitat (Narciso *et al*., 2025). Nasal inhabitation has also been confirmed for several *Ergasilus* species in both the Neotropics and Nearctic, including *E. megaceros* and *E. rhinos* from North America and *E. tipurus* from Brazil (Burris & Miller, 1972; Muzzall & Hudson, 2004; Varella *et al*., 2019).

A smaller group of genera occupy the mouth, buccal cavity, operculum or external body surface. *Paraergasilus* is predominantly nasal but may also occur in the mouth or on the gills; *Neoergasilus* may be found on fins, gills or nose; *Paeonodes* has species attached to gills, mouth and fins; and *Sinergasilus* may occur on the mouth, fins, gills or body (Yin, 1949; Pauly, 1974; Kvach *et al*., 2021; Fikiye *et al*., 2024). Four genera, *Therodamas*, *Paeonodes*, *Mugilicola* and *Majalincola* are mesoparasites that embed the cephalothorax in host tissues with the posterior trunk projecting externally, representing a distinct morphological and ecological departure from the typical ectoparasitic state (El-Rashidy & Boxshall, 2001a; Tang & Kalman, 2008).

Endoparasitism is exceedingly rare within this family and has been confirmed only for *Urogasilus*, which inhabits the urinary bladder of erythrinid and cichlid fishes in the Neotropical region. *Teredophilus* has been recorded from the pericardium or renal cavity, while *Vaigamus* remains known solely from plankton collections and has not yet been recovered from a fish host (Rancurel, 1954; Thatcher & Robertson, 1984; Rosim *et al*., 2013).

Several ergasilid species are known solely from plankton collections and have never been recorded from any host (Fellows, 1887; Kokubo, 1914; Grandori, 1925; Kuang & Li, 1984;

Thatcher & Robertson, 1984; Ranga Reddy & Kasaiah, 1994; Araujo & Boxshall, 2001; Amado & Rocha, 2001; Ohtsuka *et al*., 2004a). Despite this, they still display clear morphological adaptations for parasitism in the form of characteristic prehensile antennae. These include *Acusicola minuta* Araujo & Boxshall, 2001; *Ergasilus bani* Ohtsuka, Ho & Nagasawa, 2004; *Ergasilus chautauquaensis* Fellows, 1887; *Ergasilus divergens* (Kokubo, 1914); *Ergasilus foresti* Boxshall, Araujo & Montú, 2002; *Ergasilus genuinus* (Kokubo, 1914); *Ergasilus lagunaris* Grandori, 1925; *Ergasilus longicaudatus* Kuang & Li, 1984; *Ergasilus sergipensis* Amado & Rocha, 2001; *Paraergasilus reductus* Ranga Reddy & Kasaiah, 1994; *Pseudovaigamus spinicephalus* (Thatcher & Robertson, 1984); and *Vaigamus retrobarbatus* Thatcher & Robertson, 1984.

3.6 Lernaeidae Cobbold, 1879

The family Lernaeidae comprises one of the most specialised parasitic lineages within the cyclopoid copepods and currently includes 126 valid species in 18 recognised genera and two monophyletic lineages, the subfamilies Lamprogleninae Sproston, Yin & Hu, 1950 and Lernaeinae Wilson, 1917 (Ho, 1998; World of Copepods, accessed 2025) (Fig. 10, 11). With the sole exception of *Lamproglena lichiae* Nordmann, 1832, which has been reported from a marine fish, all species are parasites of freshwater fishes, with *Lernaea cyprinacea* Linnaeus, 1758 occasionally reported from amphibians. The family is characterised by marked sexual dimorphism. Adult females undergo a profound post-mating metamorphosis in which the cephalothorax and associated appendages are transformed into structures enabling persistent attachment to host tissues. Males retain a cyclopiform morphology and are short-lived, dying shortly after mating (Kabata, 1979; Piasecki, 1993; Boxshall & Halsey, 2004). Development proceeds through three naupliar and five copepodid stages, all of which are free living. Metamorphosis is initiated only after fertilisation, and the transformed adult female exhibits extensive modification of the anterior region in some genera. This includes formation of a holdfast used either for mesoparasitic or ectoparasitic attachment, depending on genus. Although adult females display extreme morphological diversification related to attachment mode, early developmental stages are morphologically homogeneous across the family (Boxshall & Halsey, 2004).

Some lernaeid copepods are capable of causing severe pathological effects in their hosts and may have fatal consequences, particularly under conditions of high infection intensity.

Species of *Lernaea* Linnaeus, 1758 burrow into the skin of its fish host and can cause disease called lernaeosis where haemorrhagic ulcers occur at the attachment site. Death of the host can occur due to the secondary infections and severe bleeding (Khalifa & Post, 1976; Kabata, 1984).

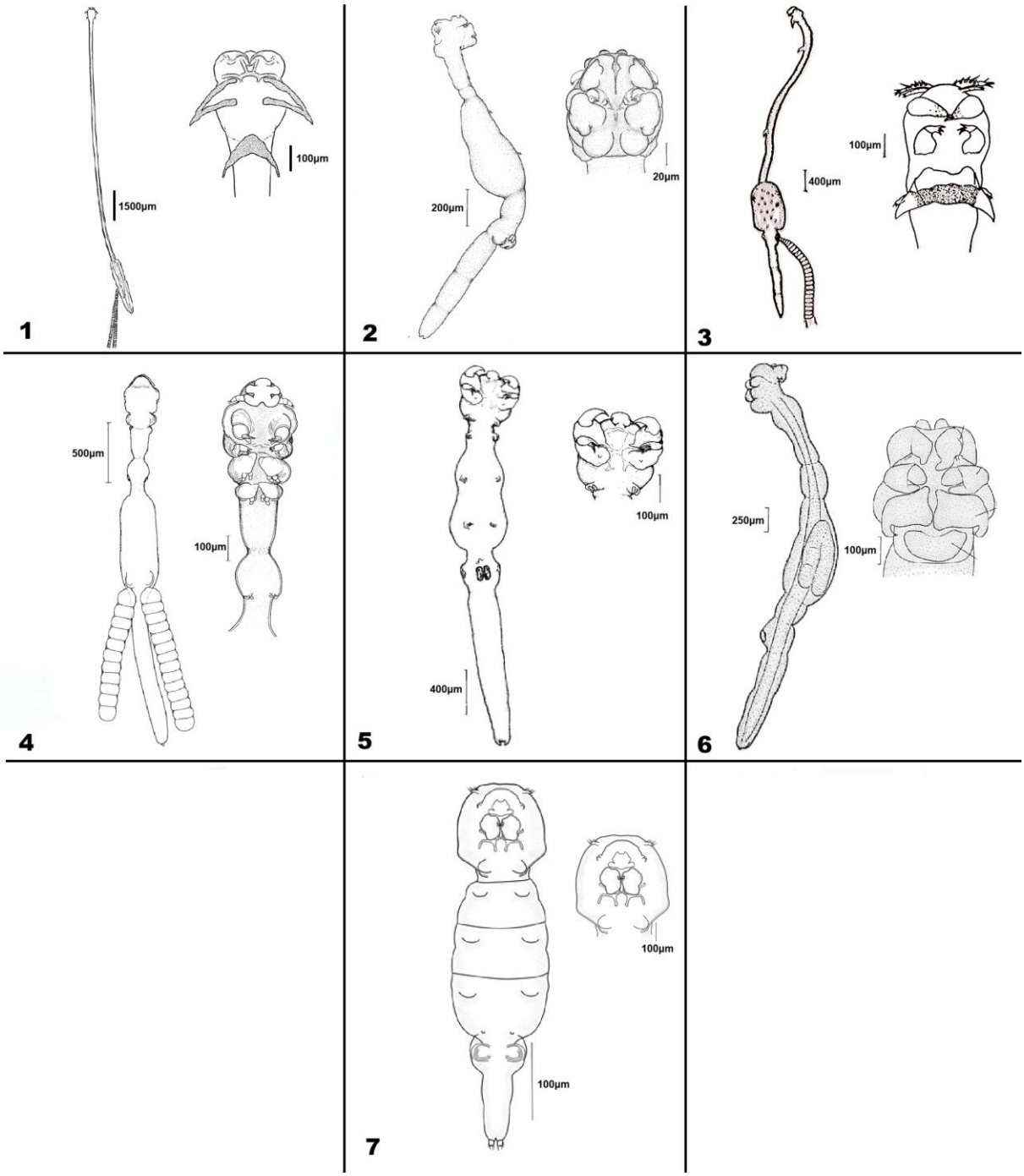


Fig. 10: Adult females of representative species from the genera of Lernaeidae and subfamily Lamprogleninae, showing general habitus and the head. (1) *Afrolernaea* Fryer, 1956; (2) *Catlaphilla* Tripathi, 1960; (3) *Indolernaea* Kabata, 1983; (4) *Indopeniculus* Kumari, Khera & Gupta, 1988; (5) *Lamproglena* von Nordmann, 1832; (6) *Lamproglenoides* Fryer, 1964; (7) *Nipergasilus* Yamaguti, 1939; (8) *Paeonodes* Wilson, 1944; (9) *Paraergasilus* Markevich, 1937. Adapted from Fryer (1956, 1964); Kabata (1983); Piasecki (1993); Ho & Kim (1997); Ho *et al*. (2009).

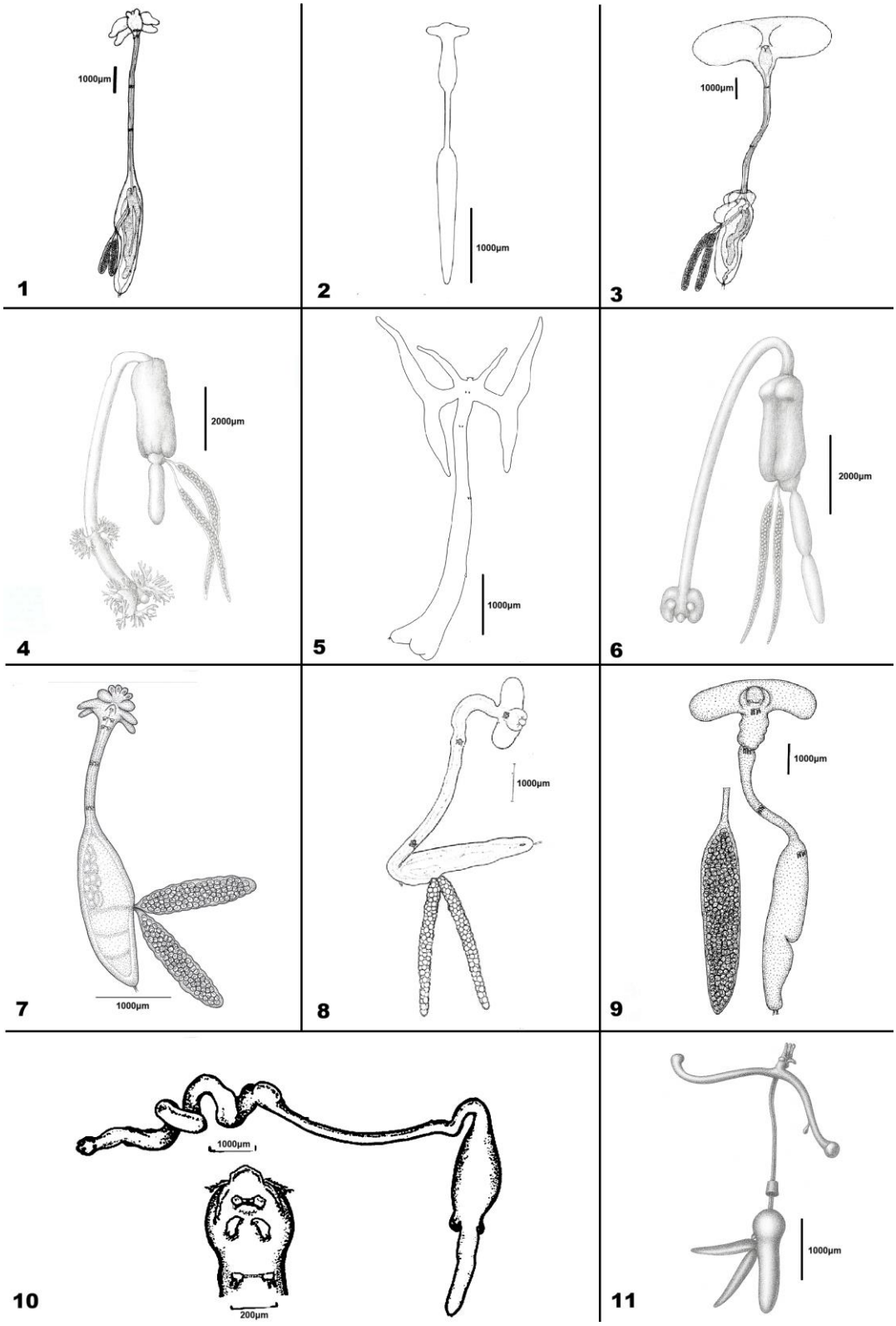


Fig. 11: Adult females of representative species from the genera of Lernaeidae and subfamily Lernaeinae, showing general habitus and the head. (1) *Amazolernaea* Thatcher & Williams, 1998; (2) *Areotrachelus* Wilson, 1924; (3) *Bedsylernaea* Thatcher & Williams, 1998; (4) *Dysphorus* Kurtz, 1924; (5) *Lernaea* Linnaeus, 1758; (6) *Lernaeogiraffa* Zimmermann, 1923; (7) *Minilernaea* Thatcher & Huergo, 2005; (8) *Opistholernaea* Yin, 1960; (9) *Perulernaea* Thatcher & Paredes, 1985; (10) *Pillainus* Kabata, 1983; (11) *Taurocheros* Brian, 1924. Adapted from Brian (1924); Kurtz (1924); Yin (1960); Kabata (1983); Thatcher & Williams (1998); Thatcher (2000); Boxshall & Halsey (2004); Thatcher & Huergo (2005).

3.6.1 History and discovery rate of Lernaeidae

Early taxonomic work on Lernaeidae began with Linnaeus, who established the genus *Lernaea* based on a parasite collected from a European cyprinid that he identified as *Cyprinus carassius* (Linnaeus, 1746). In the subsequent accounts he described an additional species from the gills of a gadid fish and later designated *L. cyprinacea* as the type species when formalising the genus in the tenth edition of *Systema Naturae* (Linnaeus, 1758). Through the eighteenth and early nineteenth centuries *Lernaea* accumulated a wide range of morphologically heterogeneous forms, because authors routinely transferred newly discovered parasitic copepods to the genus irrespective of their true affinities (e. g. Müller, 1776; Hermann, 1783; Holten, 1802; Oken, 1815; Blainville, 1822; Cuvier, 1830). This resulted in widespread taxonomic confusion, including misidentifications and inappropriate generic assignments, with several non-lernaeid taxa subsequently recognised as having been erroneously included within *Lernaea* (Wilson, 1917).

The systematic position of these parasites was long uncertain, because early authors variously assigned them to worms, molluscs or crustaceans. *Lernaea* was consistently placed among vermiform animals by Linnaeus (1746, 1758), this view was followed by several others (e. g. Müller, 1776; Schrank, 1786; Lamarck, 1816; Latreille, 1802) and retained by Cuvier (1817). Although Bosc (1801) compared *Lernaea* with *Caligus*, *Argulus* and other parasitic forms, he did not recognise their crustacean affinities. Resolution came demonstration that the egg strings of adult females contain developing embryos and that the hatched larvae correspond morphologically to *Cyclops*, thereby establishing a crustacean affinity. The conclusion was adopted by Blainville (1822), who placed *Lernaea* within Crustacea on the basis of larval characters. Subsequent nineteenth century studies supported this reassignment, but the limits of the family remained poorly defined. The family name Lernaeidae appeared only as an unaccompanied mention in Cobbold (1879) and is therefore considered a nomen nudum (World of Copepods, accessed 2025). Despite this, the name is widely used in the taxonomic and parasitological literature.

The nineteenth century also saw the establishment of *Lamproglena* von Nordmann, 1832, which became the second major genus of the family and remains one of its two most species rich lineages. During the early twentieth century several additional genera were introduced are recognised today, including *Lernaeogiraffa* Zimmermann, 1923, *Areotrachelus* Wilson,

1924, *Dysphorus* Kurtz, 1924 and *Taurocheros* Brian, 1924 (Zimmermann, 1923; Wilson, 1924a; Kurtz, 1924; Brian, 1924). Harding (1950) revised *Lernaea* and demonstrated that the extreme metamorphosis of adult females obscures diagnostic characters and the species identification should be based on premetamorphic stages, attachment sites and holdfast morphology. This study established a stable morphological framework for species recognition within *Lernaea*.

Subsequent decades introduced numerous new genera (Fig. 12), although several were later synonymised following closer morphological comparison (Fryer, 1956; Tripathi, 1960; Yin, 1960; Fryer, 1964; Boxshall, 1976; Kuang, 1980; Kabata, 1983; Thatcher & Paredes, 1985b; Kumari *et al*., 1987, 1988; Manohar *et al*., 1991). Additional genera proposed between 1950s and the early 1990s included *Afrolernaea* Fryer, 1956; *Delamarina* Dollfus, 1960; *Catlaphilla* Tripathi, 1960; *Opistholernaea* Yin, 1960; *Lamproglenoides* Fryer, 1964; *Pseudolamproglena* Boxshall, 1976; *Mesolamproglena* Kuang, 1980; *Indolernaea* Kabata, 1983; *Pillainus* Kabata, 1983; *Perulernaea* Thatcher & Paredes, 1985; *Channaculina* Kumari, Gupta & Khera, 1987; *Indopeniculus* Kumari, Khera & Gupta, 1988 and *Pseudolernaea* Manohar, Venkateshappa & Seenappa, 1991. Comparative morphological studies revealed that several of these names were junior synonyms. *Mesolamproglena* was placed in synonymy with *Pseudolamproglena* and *Channaculina* was shown to be indistinguishable from *Pillainus*, while *Pseudolernaea* was found to be identical to *Indolernaea* (Ho, 1998). *Perulernaea* lacked unique diagnostic characters separating it from *Lernaea* and was treated as a junior subjective synonym (Ho, 1998) but was considered valid again by Thatcher (2000) and Boxshall & Halsey (2004). Additional synonymies included the reduction of *Delamarina* to *Afrolernaea* (Kabata, 1983), and the synonymy of earlier names such as *Leptotrachelus* Brian, 1903 and *Silvestria* Brian, 1903 with *Areotrachelus* (Boxshall & Halsey, 2004). The enigmatic *Catlaphilla*, originally misassigned to Siphonostomatoida, was correctly recognised as a cyclopoid copepod (Manohar *et al*., 1981). The genus was poorly described and the family name Catlaphillidae rejected, the genus itself was placed a *genus inquirendum* by Boxshall & Halsey (2004), but subsequent redescription by Ho *et al*. (2009) confirmed its validity.

By the late twentieth century systematic attention shifted to the phylogenetic structure within the family. Yin *et al.* (1963) proposed three subfamilies, Lernaeinae, Lamprogleninae and Afrolernaeinae. Fryer (1968) recognised three morphological lineages, but these did not

correspond to Yin's subfamilies. Ho (1998) re-evaluated generic limits using a cladistic approach and considered several recently proposed genera invalid, while retaining support for the subfamilies. Boxshall & Halsey (2004) incorporated these results, synonymised Afrolernaeinae with Lamprogleninae, rejected proposals to elevate subfamilies to family rank (Kazachenko, 2001), and retained two currently valid subfamilies: Lamprogleninae and Lernaeinae.

Most recent studies added several Neotropical genera, notably *Amazolernaea* Thatcher & Williams, 1998, *Bedsylernaea* Thatcher & Williams, 1998 and *Minilernaea* Thatcher & Huergo, 2005. These additions increased the known Neotropical diversity (Thatcher & Williams, 1998; Thatcher & Huergo, 2005). However, relationships among the Neotropical genera remain poorly resolved because several older descriptions lack detailed information on appendage morphology.

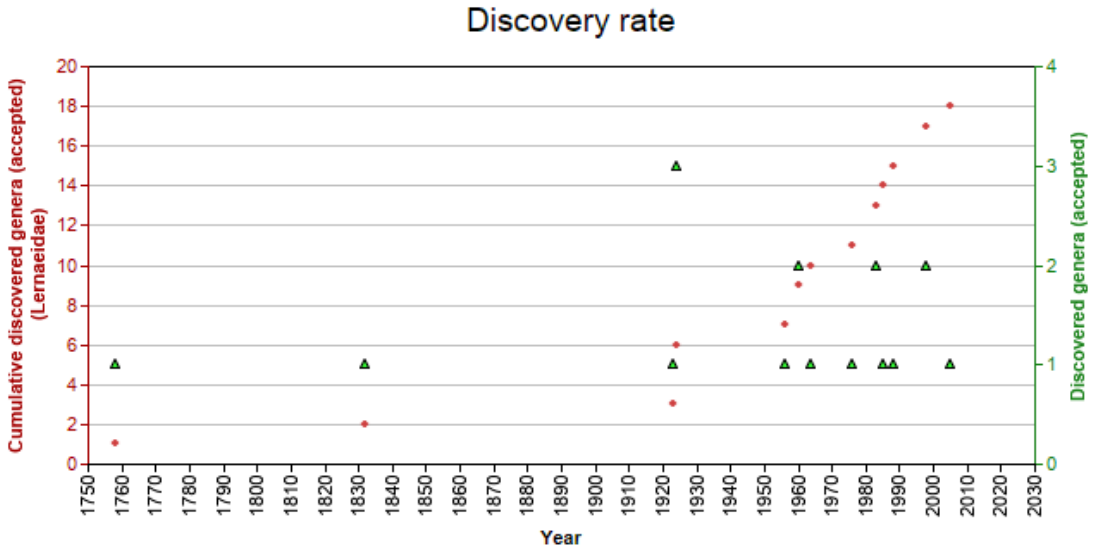


Fig. 12: Cumulative discovery rate of valid genera of Lernaeidae through time, based on data compiled from the World of Copepods database (accessed 2025).

Species level discovery in the Lernaeidae shows a similar but more coherent pattern (Fig. 13). Nineteenth century work produced only a small number of currently valid species, almost entirely within *Lernaea*, and cumulative growth remained slow until the mid-twentieth century (Cunnington, 1914; Wilson 1916, 1917, 1919, 1924b). A moderate rise followed during the 1930s to 1950s, driven by expanded sampling in Eastern Europe and East Asia (e.g. Markevich, 1936; Yü, 1937, 1938; Capart, 1943, 1944; Yin, 1948), and followed by the major revisionary output of Harding (1950), who added several morphologically distinctive *Lernaea*

specie. The steepest phase of accumulation occurred from the 1960s to the late 1990s, when systematic surveys across Africa, South America and Southeast Asia greatly expanded the known fauna and generated many new genera and species (e.g. Fryer, 1956, 1961, 1964, 1965; Yin, 1960; Kuang, 1977; Kuang & Qian, 1983, 1985; Thatcher & Paredes 1985; Oldewage, 1994; Thatcher & Williams, 1998). Several years in this period produced multiple descriptions, and the cumulative curve increased more sharply than at any earlier time. In the early 2000s the rate has slowed but remained clearly positive, with new species continuing to emerge from Neotropical, Oriental and African basins (e.g. Thatcher, 2000; Dippenaar *et al*., 2001; Jafri & Mahar, 2003, 2006; Thatcher & Huergo, 2005; van As & van As, 2007). However, in the past eighteen years only two new lernaeid species have been described, both originating from Iraq (Al-Nasiri *et al*., 2013; Míč *et al*., 2025).

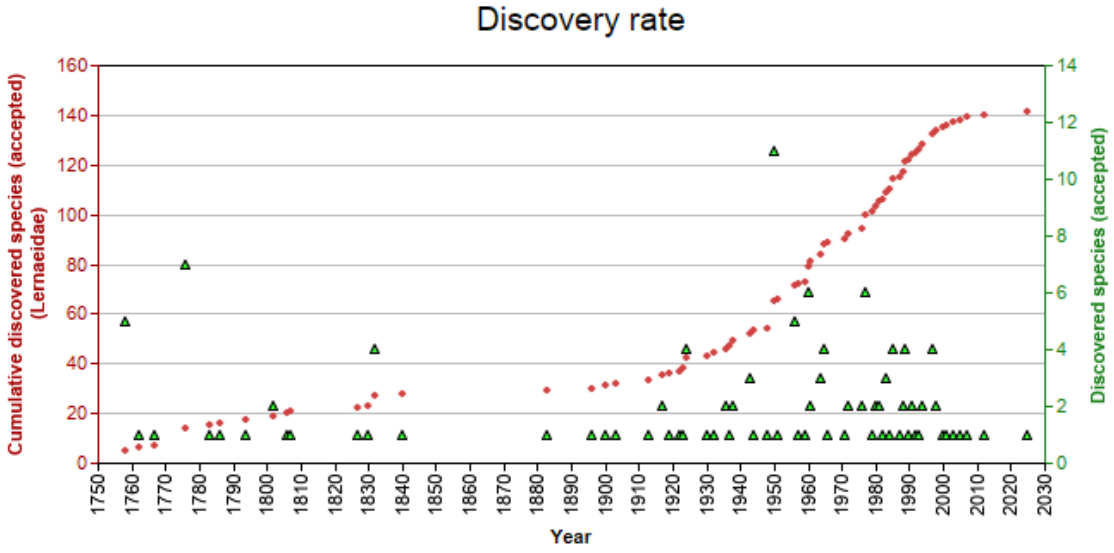


Fig. 13: Cumulative discovery rate of valid species of Lernaeidae through time, based on data compiled from the World of Copepods database (accessed 2025).

3.6.2 Host range and sites of infection in Lernaeidae

Members of the Lernaeidae are parasites of freshwater actinopterygian fishes, and several genera exhibit moderate to high host specificity, typically restricted to particular fish families or orders (Mabika *et al*., 2022; Dos Santos *et al*., 2023). The most remarkable exception is *L. cyprinacea*, which shows extremely low host specificity. This species has been reported from well over 250 freshwater fish hosts worldwide and is one of the most broadly distributed parasitic copepods. The documented host spectrum spans numerous teleost families and also

confirmed infections in amphibians including tadpoles, newts and axolotls (Waicheim *et al*., 2019; MacHale & Hedley, 2021; Varga *et al*., 2024).

Infection sites among lernaeids are highly variable and encompass nearly all external regions of the host. Many species attach to the buccal cavity and gills, while others occur on the gill rakers, operculum, fins, head or external body surface. Several species embed in the flank musculature, and produce visible inflammatory nodules, a smaller number inhabit more spatially constrained sites such as the tongue, palate or inner mouth cavity (Thatcher & Williams, 1998; Hossain *et al*., 2018). Intraspecific variation in microhabitat use is not uncommon mainly in *Lernaea*, and individuals of a single species may occur on multiple regions of the same host individual. Some other genera exhibit consistent restrictions to a single microhabitat, such as *Lamproglena* and *Pseudolamproglena* which are confined to the gills (Boxshall, 1976; Moll & Avenant-Oldewage, 2017; Kunutu *et al*., 2018).

Attachment mode in lernaeids is closely linked to morphological specialisation and strongly influences both host interaction and pathological impact. Species of *Lernaea* undergo extensive post-mating metamorphosis and develop a highly transformed cephalothoracic holdfast that anchors deeply within host tissues, producing a mesoparasitic habitus (Harding, 1950; Kabata, 1979). In contrast, members of Lamprogleninae remain ectoparasitic throughout the adult phase, adhering externally to the gills by means of enlarged, claw-like maxillae (Boxshall, 1976; Boxshall & Halsey, 2004). Despite the broad ecological variation exhibited by the family, no genuine endoparasitism has been documented in lernaeids. All taxa remain ectoparasitic or mesoparasitic, with the anterior cephalothorax embedded externally or subepidermally but not residing fully within internal organs.

3.7 Phylogenetic and molecular approaches in Ergasilidae and Lernaeidae

3.7.1 Morphological cladistics in Ergasilidae and Lernaeidae

A detailed cladistic and biogeographic study of Ergasilidae was first carried out by Amado *et al*. (1995), who tried to clarify the relationship between Ergasilidae and the then separate family Vaigamidae. Their analysis was based on the 24 type species representing the 24 valid genera recognised at that time and used 19 morphological characters, with *Anthessius* Della Valle, 1880 as outgroup (Fig. 14). Characters were based on antennule segmentation, armature and morphology of the antenna, segmentation of metasomal and urosomal somites,

and segmentation and setation patterns of the endopods of legs 1–4. The most parsimonious topology (tree length = 60; CI = 0.50; RI = 0.71) recovered eight principal clades within Ergasilidae and demonstrated that the 5 vaigamid genera *Gamidactylus*, *Gamispatulus*, *Gamispinus*, *Vaigamus* and *Pseudovaigamus* form a monophyletic cluster characterised by cephalic retrostylets and a rostral spine, nested well within Ergasilidae rather than forming a distinct family. The largest clade comprised *Rhinergasilus*, *Brasergasilus*, *Abergasilus*, *Neoergasilus*, *Nipergasilus*, *Sinergasilus*, *Ergasilus* and *Dermoergasilus*, whereas the mesoparasitic genera *Paeonodes*, *Mugilicola* and *Therodamas* clustered together with *Teredophilus* on the basis of reduction or loss of leg 5. Three Brazilian genera, *Amplexibranchius*, *Acusicola* and *Prehendorastrus*, formed another distinct clade defined by a 5-segmented antennule. Amado *et al.* (1995) interpreted their eight major clades as potential subfamilial lineages. From a biogeographical perspective, they identified the Amazon Basin as the primary centre of ergasilid diversification. At that time, 12 genera were considered endemic to this region, indicating a major Neotropical radiation.

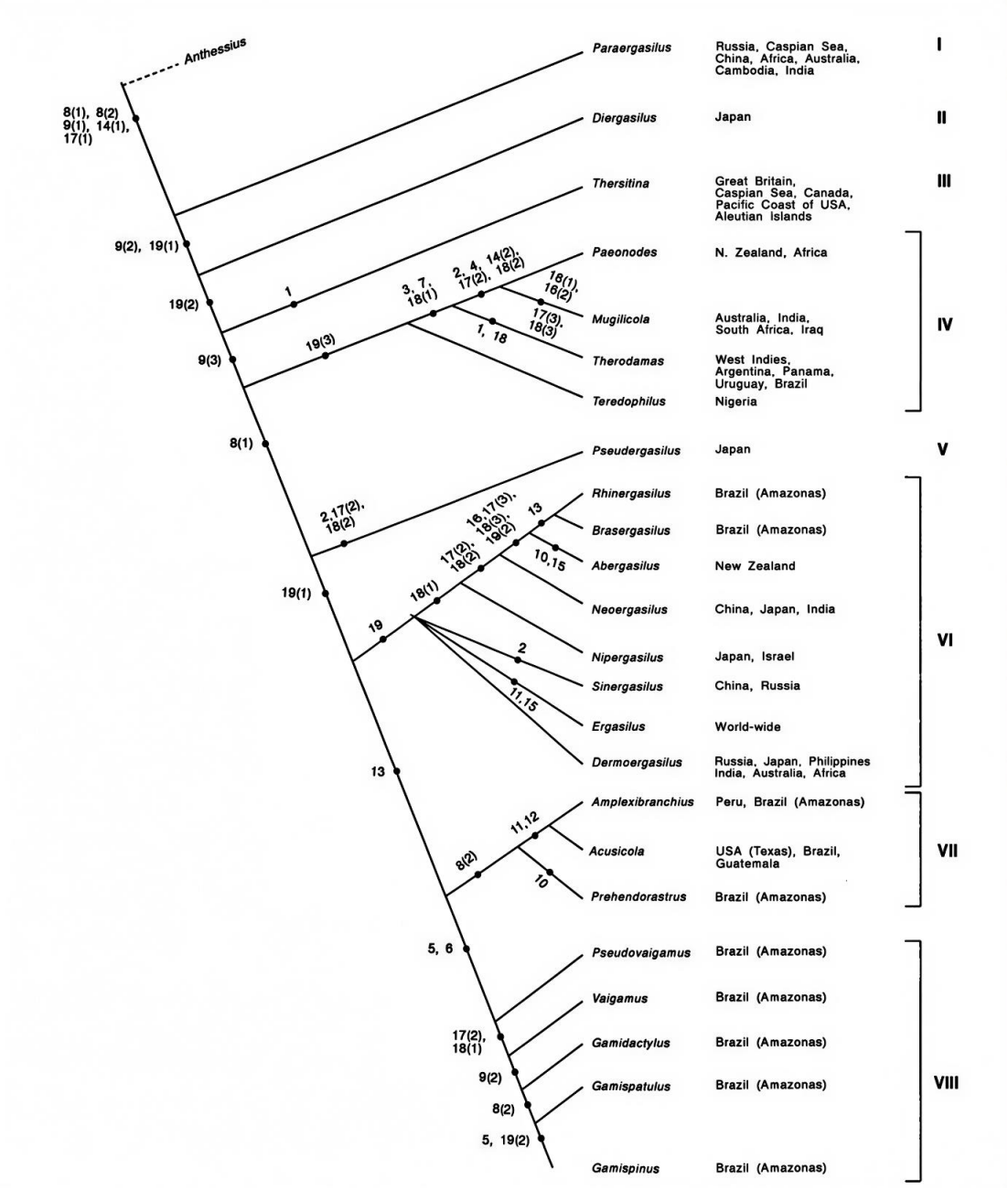


Fig. 14: Cladogram of the family Ergasilidae based on maximum parsimony analysis of morphological characters. Roman numerals denote the major clades discussed in the text. Geographic distributions of representative taxa shown to the right (reproduced from Amado *et al*., 1995).

El-Rashidy (1999) re-examined phylogenetic relationships within Ergasilidae at the species level, using an enlarged morphological character matrix and a broader taxon sample than Amado *et al.* (1995). Her consensus topology supported the monophyly of several genera, including *Neoergasilus*, *Dermoergasilus*, *Mugilicola*, *Paeonodes*, *Therodamas*, *Miracetyma*, *Brasergasilus* and *Acusicola*, whereas *Ergasilus* was shown to be highly polyphyletic and *Pseudergasilus* paraphyletic. The former vaigamids (*Gamidactylus*, *Gamispatulus*, *Gamispinus* and *Vaigamus*) formed a single monophyletic lineage, but *Pseudovaigamus* consistently

grouped within the Amazonian assemblage rather than with the other vaigamid taxa. A distinct Amazonian clade, comprising multiple Brazilian genera, was recovered and supported by segmentation characters of swimming legs. The overall analysis corroborated the evolutionary separation of many ergasilid genera and indicated that the traditional concept of *Ergasilus* does not reflect a single natural lineage and requires revision based on combined morphological and molecular evidence (Fig. 15).

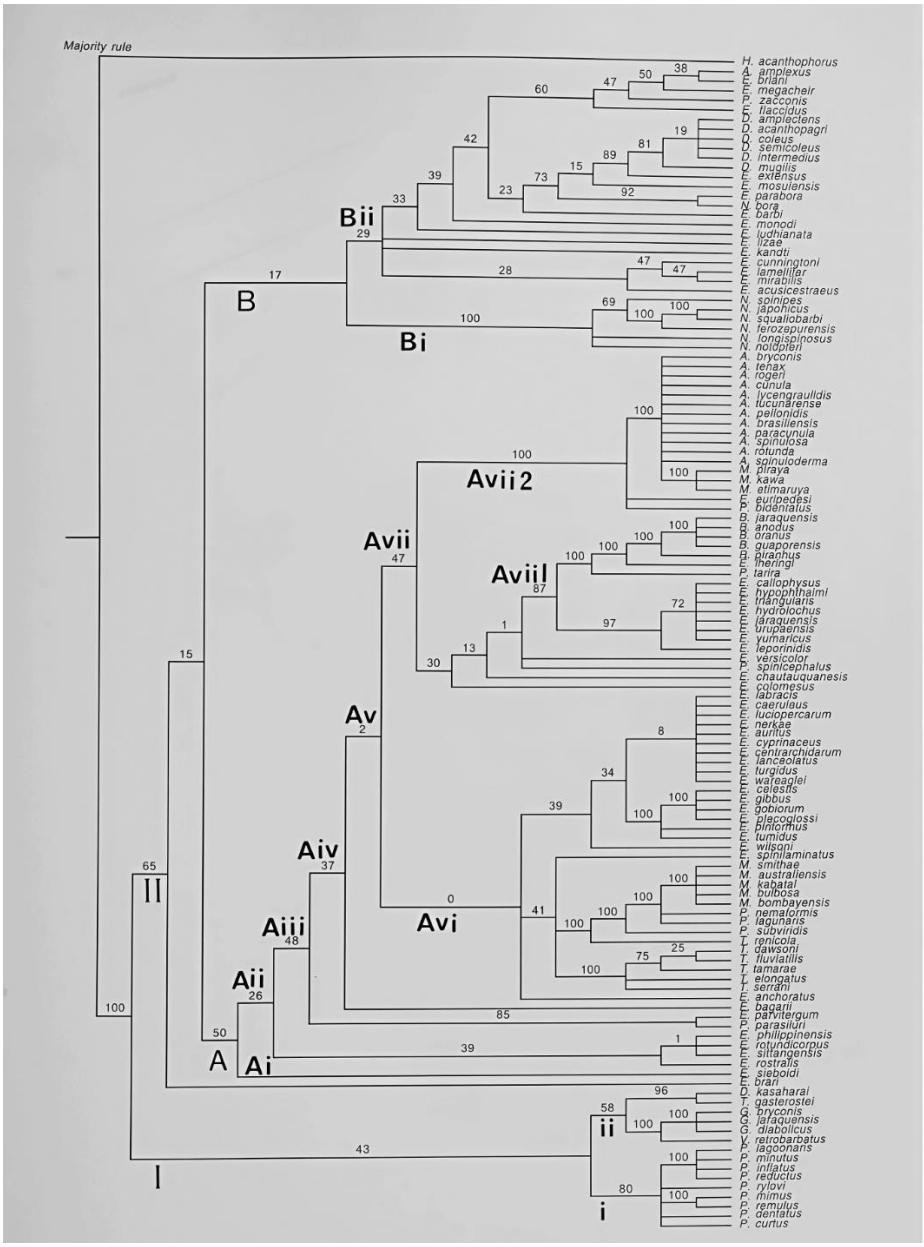


Fig. 15: Majority-rule consensus tree derived from 22,596 most parsimonious trees for the family Ergasilidae, based on 32 irreversible-up characters (reproduced from El-Rashidy, 1999).

Ho (1998) conducted a cladistic analysis of the Lernaeidae using eight ordered morphological characters of adult females and Ozmanidae as the outgroup. Two equally

parsimonious trees were obtained (length 14 steps, CI 0.92, RI 0.97), providing a working hypothesis for phylogenetic classification within the family (Fig. 16). The analysis supported the recognition of 14 valid genera at that time and divided the family into two monophyletic subfamilies: Lernaeinae, including *Areotrachelus*, *Dysphorus*, *Lernaea*, *Lernaeogiraffa*, *Opistholernaea*, *Pillainus* and *Taurocheros*, and Lamprogleninae, including *Afrolernaea*, *Catlaphilla*, *Indolernaea*, *Indopeniculus*, *Lamproglena*, *Lamproglenoides* and *Pseudolamproglena*. The two subfamilies differ consistently in antennal and maxillary armature, segmentation of appendages, and degree of cephalothoracic modification. A biogeographical area cladogram showed that the Lamprogleninae are restricted to Africa and Asia, whereas species of the Lernaeinae are more widely distributed, with endemic genera in South America. The uneven distribution was interpreted as the result of an explosive cladogenesis on the Indian subcontinent during its northward movement prior to collision with Eurasia, followed by subsequent diversification after colonisation of cyprinid fishes.

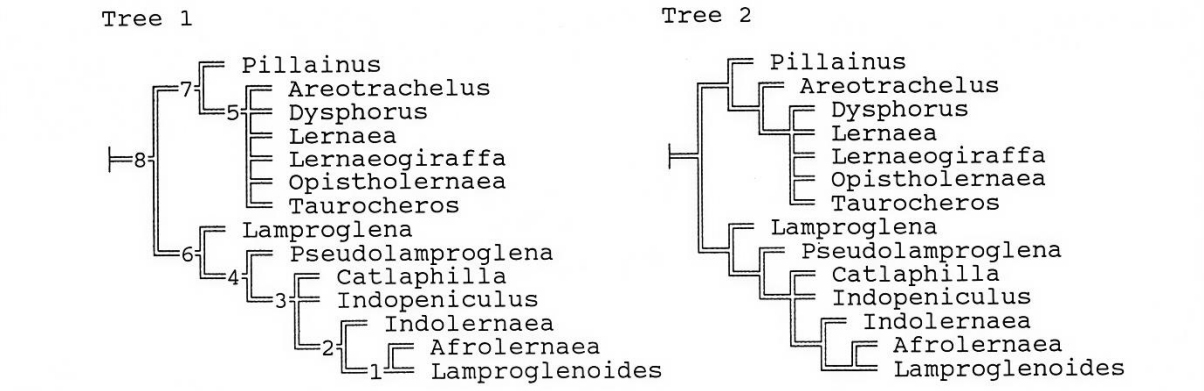


Fig. 16. Maximum parsimony trees of the Lernaeidae based on eight ordered morphological characters (Ho, 1998).

3.7.2 Molecular phylogenetics of Ergasilidae and Lernaeidae

The starting point of the molecular phylogeny era for parasitic crustaceans was a study of Kim & Kim (2000), who tried to elucidate phylogenetic relationships among poecilostome families. Phylogenetic trees were constructed by maximum parsimony, neighbour joining, and maximum likelihood methods, analyses showed that the seven poecilostome families were divided into two groups: Clausidiidae-Myicolidae-Synaptiphillidae-Bomolochidae and Lichomologidae-Chondracanthidae-Ergasilidae. Another key point was a study of Song *et al*. (2008), who provided the first phylogenetic tree for family Ergasilidae, including *Sinergasilus*,

Ergasilus, *Pseudergasilus* (now synonymized with *Ergasilus*), and *Paraergasilus* collected in China. Phylogenetic relationships were examined using neighbour-joining, maximum parsimony, maximum likelihood, and Bayesian inference methods based on partial sequences of 18S and 28S rDNA. All the analyses suggest that the *Sinergasilus* and *Paraergasilus* are both monophyletic, but the *Ergasilus* is polyphyletic rather than monophyletic. These findings also confirmed the previous cladistic analysis by El-Rashidy (1999).

Since then, many other authors have used molecular approach in their studies. Hua *et al*. (2019) raised an important question about *L. cyprinacea* and several other *Lernaea* species that might be conspecific. Santacruz *et al*. (2020) provided the first molecular data for *Acusicola* from Central America, the phylogenetic trees yielded the isolates of *Acusicola margulisae* Santacruz, Morales-Serna, Leal-Cardín, Barluenga & de León 2020 as a reciprocally monophyletic lineage, and as the sister taxa of five genera of ergasilid copepods. Kvach *et al*. (2021) published the first molecular data for *Ergasilus sieboldi* von Nordmann, 1832 and *Paraergasilus longidigitus* Yin, 1954 as native European ergasilid copepods. Phylogenetic analyses based on combined 18S and 28S rDNA showed a close relationship between *P. longidigitus* with other *Paraergasilus* species, supporting a monophyletic origin of this genus. Oliveira *et al*. (2021) described *Therodamas longicollum* Oliveira, Correa, Adriano & Tavares-Dias, 2021 from Brazil and using phylogenetic analysis they studied its divergence within family Ergasilidae and Waicheim *et al*. (2021) proved that the South American *E. sieboldi* is actually a separate species *Ergasilus yandemontei* Waicheim, Mendes Marques, Rauque & Viozzi, 2021. Míč *et al*. (2023) provided the first molecular data for *Ergasilus* in Africa, describing three new species from Lake Tanganyika. Most recently Fikiye *et al*. (2023) published the molecular data on partial 18S, 28S (rDNA), and COI (mtDNA) for *Ergasilus mirabilis* Oldewage & van As, 1987 from South Africa and Zambia. Dos Santos *et al.* (2023) genetically characterised four *Lamproglena* species from Africa (*Lamproglena clariae* Fryer, 1956; *Lamproglena hoi* Dippenaar, Luus-Powell & Roux, 2001; *Lamproglena hemprichii* von Nordmann, 1832 and *Lamproglena monodi* Capart, 1944), species appeared to be grouped more by geographical origin than host family, with *L. hoi* more closely related to other African species than to Asian species also collected from cyprinid host. The first molecular data were published by Míč *et al*. (2024) for *Dermoergasilus* and by Narciso *et al*. (2025) for *Rhinergasilus*. The invasive species *L. cyprinacea* and *Neoergasilus japonicus* (Harada, 1930)

have been sequenced multiple times from several regions (e. g. Stavrescu-Bedivan *et al*., 2014; Su *et al*., 2016; Soares *et al*., 2018; Ondračková *et al*., 2019; Kvach *et al*., 2021; Prastowo *et al*., 2023). Most recently, several Mediterranean and Middle East ergasilids and lernaeids have been sequenced, further expanding the growing phylogenetic tree (Míč *et al*., 2025). Several other sequences from unpublished data are available in databases GenBank and BOLD (mainly from plankton sampling) and are widely used in the phylogenetic trees.

3.7.3 Molecular markers and current sampling gaps

The molecular markers used in studies of parasitic copepods usually include two partial fragments of nuclear ribosomal DNA, (i.e. 18S and 28S rDNA) and mitochondrial COI. Previous phylogenetic studies confirmed that the 18S gene is more informative for resolving relationships between copepods at the genus and family levels (Huys *et al.*, 2006; Marrone *et al.*, 2013). Even though it is suitable for determining higher taxa, on the species level it does not show significant interspecific differences. This corresponds with previous studies which noted that 18S sequences are not suitable for determining the species-level richness of environmental samples, because they may underestimate species diversity (Tang *et al.*, 2012) and fail to resolve relationships between closely related species (Taniguchi *et al*., 2004). The 28S gene proves to be more informative in this respect, even though González-Orozco *et al.* (2016) reported that it has a low mutation rate and is limited in species-level identification beyond the basal branch in phylogenetic trees. The 28S rDNA sequence alone should not be used for species identification; however, in combination with a morphological description it can provide a basis for species identification (Morales-Serna *et al*., 2019). Compared with the nuclear ribosomal genes, the commonly used barcoding gene, cytochrome c oxidase subunit I (COI mtDNA), has proven useful in free-living copepods (Baek *et al*., 2016; Mayor *et al*., 2017). Moreover, COI data display high resolution at species level and may be also more efficient for revealing intraspecific variation (Tang *et al*., 2012). However, in some parasitic copepods the level of intraspecific variability is very high and complicates species boundaries, and COI sequences can be difficult to obtain consistently (Míč *et al*., 2024, 2025). Most recent evidence from parasitic copepods and marine calanoids indicates that COI remains the most informative marker for species-level delimitation, whereas 28S rRNA is more suitable for phylogenetic resolution at higher taxonomic ranks, and that both markers used jointly maximise identification accuracy (Wu *et al*., 2025).

In total, only about 3% of copepod species have been examined in a molecular phylogenetic context. Some copepod taxa have been sampled in greater detail, while others have been largely unexplored in terms of their phylogenetic relationships. The most well-sampled order of copepods is the Calanoida. The Cyclopoida, Harpacticoida, and Siphonostomatoioda require the greatest additional sampling effort, and, coincidentally, these orders contain nearly all of the parasitic copepods (Bernot *et al*., 2021).

4 MATERIAL AND METHODS

Taxonomic and phylogenetic research on parasitic cyclopoids required the integration of multiple data sources because Ergasilidae and Lernaeidae exhibit high morphological variability, wide geographical distributions, and a long history of scattered species descriptions. This dissertation therefore combines published historical records, study of specimens held in museum collections, newly collected material from Old World freshwater systems obtained during the several field trips, and molecular sequence data generated during the study period. A cumulative approach was adopted: detailed methodological procedures associated with specific datasets are presented in the individual publications of this thesis. The present chapter provides a methodological framework and explains how all datasets were integrated.

4.1 Literature survey and compilation of historical records

A comprehensive literature review was undertaken to assemble all valid records of Ergasilidae and Lernaeidae worldwide. Original species descriptions, redescriptions, parasitological surveys, checklists, and taxonomic monographs were gathered, together with subsequent revisions and taxonomic keys. Each record was evaluated for species identity, host determination, locality, site of infection, and voucher status where such information existed, and was entered into a curated working database used to evaluate global and Old World biogeographical patterns, host specificity, and species richness.

4.2 Museum and reference collections

Specimens from museum collections were examined to complement the published literature and to verify diagnostic morphological characters. Material was obtained by institutional loans and from university collections, with particular emphasis on type and historically significant specimens archived at the Natural History Museum, London, and the Royal Belgian Institute of Natural Sciences in Brussels. An extended in-person research stay at the Natural History Museum provided access to extensive historical material and original type species. Examination of this material followed standard morphological procedures and contributed to generic diagnoses.

4.3 Field sampling and morphological analyses

Specimens were collected during parasitological surveys conducted in Africa, the Mediterranean basin, and the Middle East. Detailed information on sampling sites, hosts and field protocols is provided in **Papers 1-4**. These expeditions included personal sampling in Turkey (2021-2023) and Iraq (2021) conducted in collaboration with Masaryk University and the Czech Academy of Sciences. Sampling protocols for live fish, dissection procedures, and preliminary parasite screening followed the protocols cited within the published papers.

Morphological and molecular characterisation of copepods followed procedures detaily described in **Papers 1-4**. Briefly, parasite specimens were removed from gill filaments or other attachment sites using fine needles. Specimens were mounted temporarily in GAP (glycerine–ammonium picrate) or permanently in pure glycerine and examined using an Olympus BX61 compound microscope equipped with phase-contrast optics. Line drawings were prepared with an Olympus drawing attachment and subsequently digitised using a Wacom Intuos5 Touch graphics tablet. Measurements (in µm) were taken using Olympus Stream Motion v. 1.9.3 and presented as arithmetic means followed by measured ranges and sample size. Morphological terminology follows Huys & Boxshall (1991). Host nomenclature was standardised according to the World Register of Marine Species (WoRMS). Prevalence and mean intensity of infection were calculated according to Bush *et al.* (1997). Type and voucher specimens derived from field material were deposited in the Institute of Parasitology, Biology Centre of the Czech Academy of Sciences, České Budějovice, Czech Republic. Selected specimens fixed in 70% ethanol were processed for scanning electron microscopy (SEM) using a graded ethanol dehydration series (Baltec, Liechtenstein), critical point drying, mounting on aluminium stubs, sputter coating with gold (Oerlikon Balzers), and examination under a VEGA SEM (TESCAN) operating at 5 kV (Masaryk University, Faculty of Medicine, Institute of Histology and Embryology).

4.4 Molecular and phylogenetic analyses

Genomic DNA was extracted from individual copepods or isolated egg sacs using the DNeasy Blood & Tissue Kit (Qiagen, Germany). Three genetic markers were targeted: partial fragments of 18S and 28S nuclear rDNA and a fragment of mitochondrial cytochrome c oxidase subunit I (COI). PCR amplification and sequencing protocols followed those reported

in **Papers 1-3**. Chromatograms were edited in Sequencher 4.10.1 and queried using BLASTn against the NCBI database. Newly acquired sequences were deposited in GenBank. Molecular vouchers, hologenophores and paragenophores (Pleijel *et al*., 2008) were deposited with the corresponding morphological vouchers at the Institute of Parasitology, Biology Centre of the Czech Academy of Sciences, České Budějovice, Czech Republic.

To assess phylogenetic relationships among the sampled ergasilids and lernaeids, newly generated sequences were analysed together with selected sequences retrieved from GenBank. Sequence datasets consisted of 28S rDNA for multiple species representing genera of Ergasilidae and Lernaeidae. Alignments were performed in MAFFT v. 7 (Katoh *et al*., 2019) using the G-INS-i algorithm, and ambiguous positions were refined manually in BioEdit (Hall, 1999). The optimal nucleotide substitution model was selected using ModelFinder (Kalyaanamoorthy *et al*., 2017) under the Bayesian Information Criterion. Maximum likelihood inference implemented in IQ-TREE (Trifinopoulos *et al*., 2016) used 1,000 ultrafast bootstrap replicates (Hoang *et al*., 2018), whereas Bayesian inference was performed in MrBayes 3.2.6 (Huelsenbeck & Ronquist, 2001) with two independent Markov chain Monte Carlo analyses for 10^6 generations, sampling every 100 generations and discarding the first quarter as burn-in. Tree visualisation and annotation were conducted using FigTree v. 1.4.3 (Rambaut, 2012) and Adobe Photoshop (Adobe Systems Inc., San Jose, CA, USA). Pairwise uncorrected p-distances were calculated in MEGA v. 11 (Tamura *et al*., 2021).

5 RESULTS

5.1 Overview of results

Papers 1-3 and **5** report different components of the dataset, including new species descriptions, redescriptions, new locality and host records, and molecular analyses. Together, they provide a comprehensive regional survey and form the foundation for the subsequent global review of Ergasilidae and Lernaeidae (**Paper 4**). Additional evidence for altered parasite assemblages in non-native hosts is provided by **Paper 6**, which documents reduced genetic and parasite diversity in invasive populations of *Lepomis gibbosus* in Türkiye, including record of *L. cyprinacea*.

5.2 Species of *Ergasilus* from cichlid fishes in Lake Tanganyika (Paper 1)

In **Paper 1**, a parasitological survey of cichlid fishes from the northeastern shore of Lake Tanganyika (Burundi) was conducted. From 167 examined fish belonging to 23 cichlid species, parasitic copepods were recovered from 12 host species representing 11 genera (*Bathybates*, *Ctenochromis*, *Eretmodus*, *Gnathochromis*, *Lamprologus*, *Neolamprologus*, *Ophthalmotilapia*, *Perissodus*, *Simochromis*, *Spathodus* and *Tanganicodus*). All specimens were assignable to the genus *Ergasilus* and the integrative taxonomy analyses combining morphology and partial 18S and 28S rDNA sequences confirmed the presence of five species: *Ergasilus macrodactylus* (Sars, 1909), *Ergasilus megacheir* (Sars, 1909), and three new species, *Ergasilus caparti* n. sp., *Ergasilus parasarsi* n. sp. and *Ergasilus parvus* n. sp.

The occurrence of five *Ergasilus* species within a limited sampling area along the northeastern shore of Lake Tanganyika demonstrates that the ergasilid fauna of the lake is more diverse than suggested by earlier records. Previous reports from Lake Tanganyika were restricted to a small number of nominal species described in the early to mid-twentieth century and were based solely on morphology, often from limited material (Sars, 1909; Cunnington, 1914; Capart, 1944; Fryer, 1965). None of these taxa had been re-examined using modern morphological standards or molecular data. The present results therefore indicate that ergasilid diversity in African inland waters has been underestimated, largely as a consequence of incomplete historical sampling (Fryer, 1968; Boxshall & Defaye, 2008).

Among the species recovered, *E. parvus* n. sp. exhibited the widest observed host range, occurring on seven cichlid species, whereas *E. megacheir* was rare and recorded at low

prevalence. The highest intensity of infection was observed for *E. caparti* n. sp. on *Eretmodus marksmithi*, with up to 62 individuals per host. Redescription of *E. macrodactylus* clarified several diagnostic characters that were ambiguously treated in the original account by Sars (1909), including the trapezoidal cephalosome, elongate antenna with a smooth terminal claw and three-segmented abdomen. This redescription resolves long-standing uncertainty regarding the identity of this species in Lake Tanganyika, where multiple morphologically similar ergasilids coexist. *Ergasilus megacheir* was distinguished from *E. macrodactylus* by the presence of a distinct tooth on the inner margin of the antennal claw, a short, twisted second antennal endopodal segment and a two-segmented abdomen, confirming that these taxa represent separate species despite their overall similar body form. These findings highlight the importance of detailed antennal morphology and abdominal segmentation in resolving species boundaries within *Ergasilus*, as emphasised in earlier systematic treatments (Fryer, 1968).

The three newly described species were differentiated by combinations of body size, cephalic shape, abdominal segmentation, antennal morphology and detailed spine–seta formulae of legs 1–4. *Ergasilus caparti* n. sp. is characterised by a hexagonal cephalosome, a distinctive crossed ridge indentation on the second antennal endopodal segment, a two-segmented abdomen and spinulation along the outer margins of the swimming leg rami. *Ergasilus parasarsi* n. sp. closely resembles *Ergasilus sarsi* Capart, 1944 but differs consistently in the proportions and armature of the antennal endopod, the armature of the exopods of legs 1 and 4 and the presence of spinules along the leg rami, supporting its recognition as a distinct species. *Ergasilus parvus* n. sp. is distinguished by its small body size, laterally bulged cephalosome, elongate brick-shaped egg sacs and a characteristic leg armature that separates it from the morphologically similar *Ergasilus latus* Fryer, 1960. An identification key was compiled for all *Ergasilus* species currently known from Lake Tanganyika.

Molecular analyses generated the first genetic data for African representatives of *Ergasilus*. The 18S rDNA fragment was highly conservative and showed minimal interspecific variation, whereas the 28S rDNA fragment exhibited up to 2% uncorrected p-distance among species and proved substantially more informative for species delimitation. This pattern is consistent with previous studies on ergasilids and other parasitic cyclopoids, in which 28S rDNA has been shown to provide greater phylogenetic resolution at the species and genus levels (Morales-

Serna *et al*., 2019). Phylogenetic analyses of concatenated 18S and 28S rDNA sequences recovered a well-supported clade containing all five Lake Tanganyika species, suggesting a shared evolutionary history of ergasilid lineages parasitising cichlid hosts.

Within the broader family context, tree topology was congruent with earlier molecular studies in supporting the polyphyletic status of *Ergasilus*, with the Tanganyikan clade forming one of several distinct ergasilid lineages alongside Asian *Ergasilus* groups, *Sinergasilus*, *Neoergasilus*, *Paraergasilus* and related taxa (Song *et al*., 2008). The apparent monophyly of the Tanganyikan assemblage, coupled with its association with endemic cichlid hosts, could suggest a history of local diversification within the lake. However, any real conclusions are still premature due to the lack of more ergasilid data from Africa.

5.3 New species of *Dermoergasilus* from Madagascar and Iraq (Paper 2 and Paper 5)

The results of **Papers 2** and **5** collectively expand current knowledge of *Dermoergasilus* diversity in two biogeographically distinct freshwater systems, the isolated Malagasy basins and the Mesopotamian Tigris-Euphrates drainage. In Madagascar, *Dermoergasilus madagascarensis* n. sp. was discovered during a parasitological survey of endemic freshwater fishes in four localities of north-western and eastern Madagascar, but copepods were recovered only from the cichlid *Paretroplus polyactis* in the Canal des Pangalanes. This host exhibited extremely high infection levels, with a prevalence of 90% and intensities ranging from 5 to 283 (mean 59) individuals per fish. Morphologically, the species conforms to the generic diagnosis of *Dermoergasilus* by Ho & Do (1982) through the presence of a digitiform process on caudal rami and an inflated antennal membrane, but it is distinguished from congeners such as *D. curtus* and *D. intermedius* by a pentagonal cephalosome, the ornamentation of interpodal plates, details of the genital and abdominal somites and the relative lengths of the caudal setae and digitiform processes. It also differs from the only other Malagasy parasitic copepod, D. *longiabdominalis*, which was reported from Tamatave by El-Rashidy & Boxshall (2001b). Importantly, the study provided the first molecular data for *Dermoergasilus* (18S rDNA, 28S rDNA and COI) and showed that *D. madagascarensis* n. sp. forms a clade with Palaearctic *Ergasilus sieboldi*, suggesting a possible closer relationship between some *Dermoergasilus* and *Ergasilus* lineages than might have been previously assumed.

In contrast, *Dermoergasilus planilizai* n. sp. from the abu mullet (*Planiliza abu*) in the Al-Gharraf River (Tigris system, Iraq) was detected at low prevalence (approximately 11.8%) and low mean intensity of infection (3 individuals per infected fish), despite occurring on the only freshwater mugilid native to the Mesopotamian basin. The new Iraqi species is morphologically similar to *D. varicoleus*, which has also been reported from *P. abu* and a wide range of additional hosts in the region (Ho *et al.*, 1996; Amado *et al*., 2001). However, it is consistently separable by the relative length of caudal setae and digitiform processes, the curvature of the terminal spines on the endopod of leg 1, the proportion of the free segment of leg 5 to its basal segment and distinct antennal proportions. *Dermoergasilus planilizai* n. sp. is further similar to *D. curtus*, *D. intermedius* and *D. madagascarensis* by possessing only a slightly inflated antennal membrane, and these species together may represent a structural subgroup within *Dermoergasilus* associated with freshwater or marginally brackish hosts, particularly mugilids and cichlids. Unlike the Malagasy material, no molecular sequences were obtained for the Iraqi specimens due to the preservation of the material, and the species identification relied entirely on comparative morphology.

Both studies highlight a recurrent pattern in *Dermoergasilus*, morphology is quite conservative and differences between species only subtle, mainly in the shape of cephalothorax, antennal segmentation and proportions, leg armature, caudal rami and leg 5 (Ali & Adday, 2019). These findings point to a considerable underestimation of ergasilid diversity in African, Malagasy and Mesopotamian freshwaters. Continued surveys that combine detailed morphology and molecular markers are needed for resolving species limits within *Dermoergasilus* and for clarifying the evolutionary and biogeographical relationships of this genus within Ergasilidae.

5.4 Diversity and phylogeny of parasitic copepods in the Mediterranean and the Middle East (Paper 3)

Paper 3 examined 1484 specimens belonging to 169 freshwater fish species from 155 localities across nine countries in the Mediterranean and Middle East and recovered 1004 adult female parasitic copepods from 60 host species. The material comprised seven species of Ergasilidae (*Ergasilus barbi* Rahemo, 1982; *Ergasilus briani* Markevich, 1933; *Ergasilus lizae* Krøyer, 1863; *Ergasilus rostralis* Ho, Jayarajan & Radhakrishnan, 1992; *Neoergasilus japonicus*, *Paraergasilus longidigitus* Yin, 1954 and the new species *Ergasilus italicus* n. sp.) and three

species of Lernaeidae (*Lamproglena pulchella* von Nordmann, 1832; *Lernaea cyprinacea* and the new species *Pseudolamproglena zahrziensis* n. sp.). For *E. barbi*, *E. lizae*, *E. rostralis* and *L. pulchella*, the study generated the first molecular data, while also providing new host and geographical records for all previously described species.

Ergasilus briani emerged as the most abundant and widespread ergasilid, with new country records from Bosnia and Herzegovina, Croatia, Albania and Greece, and a wide host range on cyprinids and leuciscids. This pattern is consistent with earlier reports that *E. briani* is widely distributed across the Palaearctic (Alston *et al*., 1993) but may have been under-recorded due to uneven sampling intensity and limited parasitological surveys in southern Europe and the Balkans. *Ergasilus barbi*, previously known only from Iraq, was newly recorded in Turkey, similarly to a very closely related Middle Eastern *Ergasilus mosulensis* and both have wider regional distributions than originally assumed (Rahemo, 1982; Öktener *et al*., 2009). *Ergasilus rostralis* was confirmed from Iraq at low intensities in agreement with earlier reports of occurrence and a broad host spectrum in the region (Khamees *et al*., 2015; Mhaisen & Al-Daraji, 2023). *Ergasilus lizae* was found in brackish-influenced reaches of the Sperchios River in Greece, with a possibility that it may represent a complex of cryptic species rather than a cosmopolitan species (Kabata, 1992; El-Rashidy, 1999; Morales-Serna *et al*., 2024). *Neoergasilus japonicus* exhibited the widest host range within Ergasilidae (14 host species) and extended its known distribution to Croatia and Iraq, reinforcing its status as a widely dispersed generalist and invasive parasite (Ondračková *et al*., 2025). *Paraergasilus longidigitus* was newly recorded from Albania in low abundance and exclusively from the nasal cavity, a microhabitat that likely contributes to its under-reporting in routine parasitological surveys (Koyun *et al*., 2007; Kvach *et al*., 2021). Within Lernaeidae, *Lernaea cyprinacea* was confirmed as a widely distributed, invasive cosmopolitan parasite throughout the Mediterranean and Middle East, showing extremely low host specificity and high ecological plasticity, consistent with its global invasion history (Avenant-Oldewage, 2012; Waicheim *et al*., 2019). *Lamproglena pulchella* also showed a wide host range (19 host species) and distribution, with several closely related 28S rDNA variants suggesting a possible cryptic species complex. *Pseudolamproglena zahrziensis* n. sp. was described from *Carasobarbus luteus* in Iraq as the fifth species of the genus and the third reported from the country, further emphasising the

Middle East as a centre of diversity for several lineages (Boxshall, 1976; Al-Nasiri *et al*., 2013; Mhaisen *et al*., 2024).

Phylogenetic analyses based on 28S rDNA resulted in six well-supported ergasilid clades and two major lernaeid clades corresponding to subfamilies Lamprogleninae and Lernaeinae, previously established by Wilson (1917) and Sproston *et al*. (1950). *Ergasilus italicus* n. sp., together with *E. barbi*, *E. lizae*, *E. rostralis* and several African and Asian *Ergasilus* species, formed clade A, which includes lineages from African cichlids, catfishes and cyprinids. This could suggest an evolutionary link between Mediterranean, Middle Eastern and African ergasilids. *Ergasilus briani* and *N. japonicus* clustered in clade B, with *E. briani* grouping with Chinese *Ergasilus* species and *N. japonicus* forming a separate *Neoergasilus* subclade that retained two previously known rDNA variants without any morphological differentiation (Ondračková *et al*., 2019). Within Lernaeidae, all genetic variants of *L. pulchella* and *P. zahrziensis* n. sp. clustered with several African *Lamproglena* species sequenced previously (Mabika *et al*., 2022; Rindoria *et al.*, 2023; Dos Santos *et al.*, 2023). This could suggest that *Pseudolamproglena* species are actually highly modified *Lamproglena*, although additional molecular data is needed to confirm this and the genus is retained valid. *Lernaea cyprinacea* grouped with several other nominal *Lernaea* species that were not genetically distinct at rDNA markers, reconfirming serious doubts about current species boundaries (Hua *et al*., 2019).

The study shows that even in relatively well-studied regions such as the Mediterranean and Middle East, the diversity, host ranges and phylogenetic relationships of ergasilid and lernaeid copepods remain incompletely resolved and deserve further attention.

5.5 Global diversity and biogeography of Ergasilidae and Lernaeidae (Paper 4)

Paper 4 presents the first comprehensive global review of parasitic copepods of the families Ergasilidae and Lernaeidae, compiling all published records from original descriptions to the present. A standardised database was assembled from historical and contemporary literature, integrating taxonomic status, host associations, biogeographical distribution and available molecular data.

The review recognises 284 valid species of Ergasilidae assigned to 29 genera and 126 valid species of Lernaeidae assigned to 18 genera worldwide. Ergasilids are recorded from at least 55 host orders, 152 host families and more than 750 host species, whereas lernaeids parasitise

at least 32 host orders, 78 host families and more than 470 fish species, with occasional records from amphibians. Twelve ergasilid species are known exclusively from planktonic material and have never been recorded from hosts.

Species richness shows strong geographical structuring. Ergasilidae attain their highest diversity in the Neotropical region (102 species, 19 genera), followed by the Oriental (75 species), Palaearctic (72 species), Afrotropical (33 species) and Nearctic (33 species) regions, with markedly reduced richness in Australasia and the Pacific Oceanic Islands (Paper 4, Fig. 1). This pattern is consistent with earlier review of freshwater copepod diversity, which identified the Neotropics, and particularly the Amazon Basin, as a major centre of endemic radiation for multiple copepod lineages, including parasitic taxa (Boxshall & Defaye, 2008). In contrast, Lernaeidae reach peak diversity in the Oriental (58 species, 9 genera) and Afrotropical (43 species, 7 genera) regions, with comparatively low representation in the Neotropics, Nearctic and Australasia, and no confirmed records from the Pacific Oceanic Islands (Paper 4, Fig. 2). This distribution has long been attributed to an early radiation of lernaeids associated with cyprinid hosts in Asia, followed by dispersal into Africa and Eurasia, a hypothesis previously outlined by Ho (1998) and supported by the concentration of endemic genera in these regions.

Host association analyses reveal strongly uneven host representation in both families. In Ergasilidae, Cypriniformes represent the most frequently parasitised order, followed by Siluriformes, Cichliformes and Characiformes, whereas Lernaeidae show an even stronger dominance of cypriniform hosts, which account for nearly half of all recorded host occurrences. Most species in both families are recorded from a single or few hosts, a pattern that largely reflects uneven sampling intensity and the predominance of species known only from original descriptions or limited material. As a result, robust assessment of host specificity remains difficult for the majority of taxa. Broad host generalism is restricted to a small number of widely distributed species. The species of *N*. *japonicus* and *L*. *cyprinacea* are recognized as globally invasive parasites whose anthropogenic dispersal has substantially altered their distribution patterns (Ondračková *et al*., 2025). *Lernaea cyprinacea* exhibits the widest host range documented for any freshwater parasitic copepod, with records from more than 270 host species across over 30 orders and with reports from all continents except of Antarctica.

Molecular data remain limited and unevenly distributed. Sequence data are available for 47 ergasilid species (13 genera) and 13 lernaeid species (3 genera), representing

approximately 14% of Ergasilidae and 10% of Lernaeidae diversity. Comparable limitations in phylogenetic coverage still constrain higher level interpretations within copepods, with only a fraction of species sequenced (Bernot *et al*., 2021). Available phylogenetic evidence confirms the polyphyly of *Ergasilus*, highlights unresolved generic boundaries within both families, and indicates possible cryptic diversity in several widely reported species. However, the current molecular coverage remains insufficient to support robust conclusions regarding higher-level relationships or taxonomic restructuring. Many genera are represented by one or a few sequenced species only, and large portions of both families remain entirely unsampled at the molecular level. Any major taxonomic changes based on the existing phylogenetic framework would be premature and would likely increase, rather than reduce, instability within an already complex and heterogeneous classification.

In addition to compiling global diversity and distributional data, **Paper 4** also formalised several taxonomic changes. These included new generic combinations, replacement names and the exclusion of problematic nominal taxa, with the aim of standardising nomenclature and aligning historical records with current morphological and phylogenetic evidence. Summary tables of species richness by genus and biogeographical region are provided, together with complete species-level tables documenting valid names, synonymies, host associations and verified distribution records.

6 CONCLUSION AND FUTURE PROSPECTS

This thesis advances current knowledge of the diversity, taxonomy, phylogeny and biogeography of freshwater parasitic copepods of the families Ergasilidae and Lernaeidae, with primary emphasis on Old World regions of Africa, the Mediterranean region and the Middle East. By combining original faunistic surveys, integrative taxonomic analyses and a global synthesis of published records, it addresses persistent gaps in both regional and global understanding of these groups.

At the regional scale, the results demonstrate that substantial parasite diversity remains undocumented in freshwater systems. The survey of Lake Tanganyika revealed a richer ergasilid fauna than previously recognised, including three new species of *Ergasilus* and the first molecular data for African representatives of the genus. These findings indicate that even historically intensively studied lake systems can harbour overlooked parasite diversity.

Similarly, the description of new *Dermoergasilus* species from Madagascar and Iraq highlights the persistence of undescribed lineages in isolated island systems and in the Mesopotamian basin, regions that remain taxonomically fragmented and incompletely sampled.

The broad survey of the Mediterranean and Middle East confirms that parasitic copepod diversity, host associations and distributions remain incompletely documented even within the Palaearctic. Numerous new host and country records were established, two additional species were described and molecular data were generated for several taxa previously lacking sequence information. Phylogenetic analyses consistently supported the polyphyly of *Ergasilus*, revealed unresolved generic boundaries in both families and indicated possible cryptic diversity in widely reported taxa such as *Lamproglena pulchella* and *Lernaea cyprinacea*.

At the global scale, the synthesis presented in Paper 4 constitutes the first comprehensive review of Ergasilidae and Lernaeidae worldwide. It provides a baseline for assessing species richness, host associations and geographical distributions. The review reveals pronounced geographical bias in sampling effort, a predominance of species known only from original descriptions and a severe shortage of molecular data, indicating that current diversity estimates should be taken as conservative. The global review also formalised a series of necessary taxonomic adjustments, including new combinations, replacement name and the exclusion of problematic nominal taxa. This has been done to stabilise nomenclature and reconcile historical literature with current morphological and phylogenetic evidence. These changes establish a consistent framework for future work but do not represent a definitive taxonomic resolution.

Across all studies, limited and uneven molecular coverage emerged as a major constraint. Only a small proportion of described species has been sequenced so far, many genera are represented by one or a few taxa, and existing datasets are insufficient to support large-scale taxonomic restructuring. Any comprehensive revision will require targeted taxon sampling and the application of multiple independent genetic markers combined with careful morphological evaluation.

Finally, the thesis highlights the influence of host movements on present-day parasite distributions. Widely dispersed species such as *Neoergasilus japonicus* and *Lernaea*

cyprinacea illustrate how anthropogenic translocations can obscure historical biogeographical patterns and facilitate global spread. Distinguishing native distributions from recent introductions remains problematic in many regions.

Future progress will depend primarily on improved biogeographical coverage and more balanced sampling across poorly studied regions. Most genera remain only known from limited material, and integrative studies combining detailed morphology with expanded molecular datasets will be required to stabilise species boundaries and evaluate phylogenetic hypotheses.

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8 APPENDIX

Paper 1

Míč, R., Řehulková, E., & Seifertová, M. (2023). Species of *Ergasilus* von Nordmann, 1832 (Copepoda: Ergasilidae) from cichlid fishes in Lake Tanganyika. *Parasitology*, *150*(7), 579-598. https://doi.org/10.1017/S0031182023000239

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Species of *Ergasilus* von Nordmann, 1832 (Copepoda: Ergasilidae) from cichlid fishes in Lake Tanganyika

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Abstract

Ergasilus (von Nordmann, 1832) (Ergasilidae) is a species-rich group of parasitic copepods with a wide distribution in freshwater, marine and brackish environments. Up to now, 9 species of *Ergasilus* are known from cichlid fishes in Africa. In this study, 5 species, including 3 new, were collected from the gills of 12 cichlid species (11 genera: *Bathybates*, *Ctenochromis*, *Eretmodus*, *Gnathochromis*, *Lamprologus*, *Neolamprologus*, *Ophthalmotilapia*, *Perissodus*, *Simochromis*, *Spathodus* and *Tanganicodus*) of the northeastern shore of Lake Tanganyika in Burundi, namely *E. macrodactylus* (Sars, 1909), *E. megacheir* (Sars, 1909), *E. caparti* n. sp., *E. parasarsi* n. sp. and *E. parvus* n. sp. All species found were identified and described on the basis of adult female specimens using an integrative taxonomy approach mixing morphological characterization and molecular analyses of 2 ribosomal DNA markers (partial 18S and 28S rDNA sequences). An identification key for *Ergasilus* species from Lake Tanganyika is included. This study provides the first molecular data for *Ergasilus* species in Africa. The phylogenetic analyses suggest that the *Ergasilus* species parasitizing Lake Tanganyikan cichlids form a well-supported clade within the Ergasilidae. However, their phylogenetic relationships with other congeners still remain unclear due to a lack of molecular data for this diverse genus.

Introduction

Lake Tanganyika, one of the largest (32 900 km^2) tropical lakes and the oldest (~9–12 Ma) of the East African Great Lakes (Cohen *et al.*, 1993), represents a unique freshwater ecosystem characterized by high levels of species richness and a high degree of endemism. Therefore, it has received an intensive interest from scientists of various fields for decades (e.g. Kmentová *et al.*, 2018; Rahmouni *et al.*, 2018; Koblmüller *et al.*, 2019; Ryan *et al.*, 2020; Ivory *et al.*, 2021). In this respect, cichlids (Cichlidae) have become one of the most studied model systems in the research on evolutionary processes, speciation events (e.g. Hayward *et al.*, 2017; Irisarri *et al.*, 2018; Fischer *et al.*, 2021) and behavioural biology (e.g. Raffini *et al.*, 2018; Satoh *et al.*, 2019, 2022). Currently, 240 valid cichlid species belonging to 52 genera and 13 tribes are described from Lake Tanganyika; all (except 2 species) are endemic to the basin (Ronco *et al.*, 2021) and comprise the morphologically, behaviourally and ecologically most diverse species assemblage (Snoeks, 2000). It is not surprising then that cichlid fishes have also become a suitable model for studies of host–parasite systems. In recent years, the most studied fish parasites from Lake Tanganyika have been, in particular, Monogenea (e.g. Vanhove *et al.*, 2015; Rahmouni *et al.*, 2017, 2018), in contrast to parasitic crustaceans that have been neglected for decades, not only in Lake Tanganyika but in Africa overall (Scholz *et al.*, 2018).

Ergasilus (von Nordmann, 1832) represents the type and most speciose genus of the family Ergasilidae (Burmeister, 1835), with approximately 160 nominal species worldwide, inhabiting fresh, marine and brackish waters (Boxshall and Defaye, 2007; WoRMS Editorial Board, 2022). In recent years, the majority of systematic studies dealing with ergasilid species originated from the Neotropical region (Marques *et al.*, 2015; Muriel-Hoyos *et al.*, 2015; Taborda *et al.*, 2016; Varella *et al.*, 2019; Narciso *et al.*, 2020; Santacruz *et al.*, 2020; Waicheim *et al.*, 2021), which is in contrast to Africa, where no new records have been available in the past few decades. The first studies of African Ergasilidae were conducted between 1900 and 1928 in the African Great Lakes (Sars, 1909; van Douwe, 1912; Cunnington, 1920; Gurney, 1928), while the first description of *Ergasilus* species from Africa was made by Sars (1909), who described 3 species (originally assigned to the currently invalid genus *Ergasiloides*) from Lake Tanganyika. From the 1920s to the late 1960s, the next occurrences of *Ergasilus* species were reported in large African river systems such as the Niger River (Capart, 1956), the Volta (Paperna, 1969), the Congo (Fryer, 1963, 1967), the White Nile (Wilson, 1924) and the lakes (Albert, Edward, Kivu, Malawi, Rudolf, Tanganyika and Victoria) (Fryer, 1956, 1960, 1961, 1965). To date, 11 valid species of *Ergasilus* are described from the gills of 13 families of freshwater fishes from Africa, 5 of them recorded on cichlids, mochokids and poeciliids from Lake Tanganyika: *E. flaccidus* Fryer, 1965; *E. kandti* van Douwe, 1912; *E. macrodactylus* (Sars, 1909); *E. megacheir*

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(Sars, 1909); and *E. sarsi* Capart, 1944 (Sars, 1909; Cunnington, 1914; Capart, 1944; Fryer, 1965; Oldewage and van As, 1988; Kilian and Avenant-Oldewage, 2013; Smit and Hadfield, 2018). However, since Fryer's research (1965, 1968), records of ergasilids from Lake Tanganyika are scarce. Kondo and Hori (1986) and Raeymaekers *et al.* (2013) reported unidentified species of the genus *Ergasilus* in the southern end of Lake Tanganyika, but no morphological determination was provided in either of the studies. The last study that included ergasilids from Tanganyika was by Kilian and Avenant-Oldewage (2013) that reported the first record of *E. sarsi* from Tanganyika killifish and provides a description of the pathological alterations caused by this species. Nevertheless, over the last 30 years, the interest in Ergasilidae in Africa has declined. This suggests that the ergasilid fauna in Africa is still largely underexplored and that its intensive investigation is therefore needed.

Moreover, all previous records of *Ergasilus* species are based solely on morphometric data. Until recently, the majority of available molecular data for *Ergasilus* came from Song *et al.* (2008), who provided the first phylogenetic analysis of the family Ergasilidae (comprising 14 species collected in China) and proposed a polyphyletic origin for this genus. Molecular data for the African ergasilids are still completely lacking. Such data would help to resolve the taxonomical and phylogenetic relationships poorly known in this highly diverse parasitic group.

During our parasitological survey of metazoan parasites of cichlids from Lake Tanganyika, we recovered 2 previously described and 3 new *Ergasilus* species. All species found were described using a combined morphological and molecular approach as an integrative taxonomy, a recent trend that promises to complete dubious and precise descriptions and other taxonomic problems. Additionally, the phylogenetic relationships among ergasilids from Lake Tanganyika cichlids were investigated on the basis of rDNA sequence data (partial 18S and 28S rDNA).

Materials and methods

Fish collection

During a parasitological survey in 2013, 23 species (167 specimens) of cichlid fishes, representing 11 tribes, were bought from a local fish market in Bujumbura (3°23′S, 29°22′E) or obtained from commercial fishermen fishing in 4 localities on the northeastern shore of Lake Tanganyika in Burundi: (1) Magara (3°44′S, 29°19′E); (2) Mukuruka (4°14′S, 29°33′E), (3) Mvugo (4°15′S, 29°34′E) and (4) Nyaruhongoka (3°41′S, 29° 20′E) (Fig. 1, Table 1). The determination of cichlid hosts was provided by Dr Stephan Koblmüller (The University of Graz, Austria) using the keys of Takahashi (2003) and Takahashi and Koblmüller (2011). Live fish specimens were killed by severing the spinal cord and were subsequently processed for parasitological examination. The scientific names of fish hosts follow Froese and Pauly (2022).

Parasite collection and identification

The body surface, gills and nasal cavities of freshly killed fishes were examined for the presence of parasitic copepods using a dissecting microscope. Live copepods were collected from the gills using fine needles and were fixed in 70% ethanol for later morphological examination, or in 96% ethanol for molecular analysis. In addition, a subset of specimens collected for DNA analyses were dissected and the egg sac or a small part of the body were cut off using fine needles under a dissecting microscope and used for DNA extraction; the rest of the body was used for morphological evaluation as hologenophore. For the morphological determination of copepods, specimens were placed on a microscopic slide in a drop of water with lactic acid to clear and soften them. The selected crustaceans were then fixed in pure glycerine (Dávidová and Smit, 2018) or glycerine ammonium picrate and examined. The mounted specimens were studied using an Olympus BX61 microscope equipped with phase-contrast optics. Drawings of the copepods were made using an Olympus drawing attachment and edited with a graphic tablet (Wacom Intuos5 Touch) compatible with Adobe Illustrator and Adobe Photoshop (Adobe Systems Inc., San Jose, CA, USA). All measurements (in micrometres) were taken using a digital image analysis software (Olympus Stream Motion v. 1.9.3) and are presented as mean followed by range and number (*n*) of specimens measured in parentheses. *Ergasilus* species were determined according to Oldewage and van As (1988) on the basis of the shape and size of the body, the antennae, the antennules, the cephalothorax, pigmentation, the setae and spines on legs I–IV, rudimentary leg V, the genital somite, the furcal rami and the shape of the egg sac. Morphological terminology follows that of Huys and Boxshall (1991).

For comparative purposes, specimens of the following 7 previously described species of *Ergasilus* from the Natural History Museum (London, UK; BMNH) and Royal Belgian Institute of Natural Sciences (Bruxelles, Belgium; RBINS COP) were examined:

E. cunningtoni Capart, 1944 (BMNH 1950.7.29.23); *E. flaccidus* Fryer, 1965 (BMNH 1965.10.6.1); *E. kandti* Douwe, 1912 (BMNH 1998.929-930); *E. lamellifer* Fryer, 1961 (BMNH 1998.931); *E. latus* Fryer, 1960 (BMNH 1993.122-131); *E. macrodactylus* (Sars, 1909) (COP 6086, COP 6087, COP 6088, COP 6089); and *E. sarsi* Capart, 1944 (COP 0493, COP 0494).

The type and voucher specimens of the copepods collected in the present study were deposited in the Institute of Parasitology, Czech Academy of Sciences, České Budějovice, Czech Republic. Prevalence (percentage of infected fish) and mean intensity of infection (mean number of parasites per infected host) were calculated for each *Ergasilus* species found following Bush *et al.* (1997).

Molecular and phylogenetic analyses

Genomic DNA was isolated separately from each parasite specimen (or its part) using DNeasy®Blood & Tissue Kit (Qiagen, Hilden, Germany) according to the manufacturer's instructions. To perform molecular characterization of the species found and to elucidate their phylogenetic position within Ergasilidae, 2 ribosomal nuclear fragments (18S rDNA and 28S rDNA) were analysed. Partial 28S rDNA fragment was amplified using primers 28SF (forward, 5′-ACA ACT GTG ATG CCC TTA G-3′) and 28SR (reverse, 5′-TGG TCC GTG TTT CAA GAC G-3′) (Song *et al.*, 2008). Primers 18SF (forward, 5′-AAG GTG TGM CCT ATC AAC T-3′) (Song *et al.*, 2008) and 18SR (reverse, 5′-TTA CTT CCT CTA AAC GCT C-3′) (Song *et al.*, 2008) were used for amplification of the partial fragment of 18S rDNA. In addition, the newly designed primers Erg18SF1 (forward, 5′-ATT GGA GGG CAA GTC TGG TG-3′), Erg18SF2-int (forward, 5′-CGA TCA GAT ACC GCC CTA GT-3′) and Erg18SR2 (reverse, 5′-AAG GGC AGG GAC GTA ATC AA-3′) were used for amplifications of the 18S rDNA fragment when the first combination of primers failed. All PCRs were carried out in a total volume of 20 μL containing 3 μL of DNA extract, 1× PCR buffer (Fermentas, Waltham, MA, USA), 2 mM $MgCl_2$, 200 μM of each dNTP, 0.2 μM of each primer and 1 U of Taq polymerase (Fermentas). Amplification was performed under the following conditions: 94°C for 5 min; 39 cycles of 94°C for 30 s; an annealing temperature of 54°C for 30 s; and 72°C for 1 min, with a final

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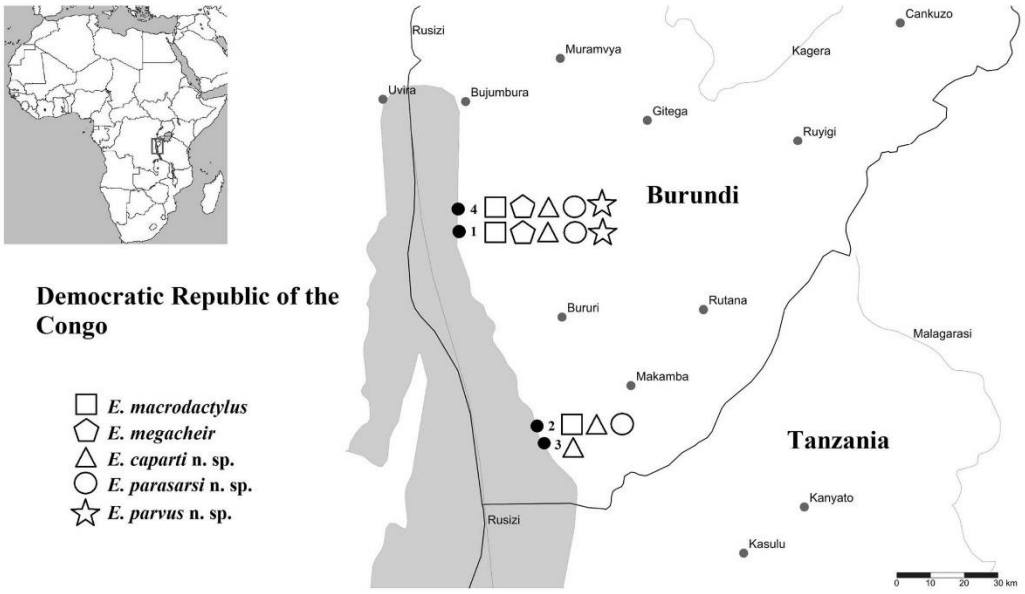


Fig. 1. Map of Lake Tanganyika indicating the sampling localities along the northeastern shore in Burundi: (1) Magara; (2) Mukuruka; (3) Mvugo; (4) Nyaruhongoka.

extension step at 72°C for 5 min. The PCR amplicons were checked by electrophoresis on 1.5% agarose gels stained with GoodView™ (Amplia s.r.o., Bratislava, Slovakia), and PCR products of the required length were purified using ExoSAP-IT™ (Affymetrix Inc., Santa Clara, USA), following the manufacturer's instructions. Purified products were directly sequenced using the same primers as those for PCR. DNA sequencing was carried out using BigDye® Terminator v3.1 Cycle Sequencing Kit (Applied Biosystems by Thermo Fisher Scientific, Prague, Czech Republic) and a 3130 Genetic Analyzer (Applied Biosystems). The obtained sequences were assembled and edited using Sequencher software (Gene Codes Corp., Ann Arbor, MI, USA). Newly generated sequences for each species were deposited in GenBank under accession numbers OQ407470–OQ407474 (28S rDNA) and OQ407465–OQ407469 (18S rDNA), and molecular vouchers (hologenophores, paragenophores; Pleijel *et al.*, 2008) were deposited in the Institute of Parasitology, Czech Academy of Sciences, České Budějovice, Czech Republic.

To investigate the phylogenetic position of copepods of Lake Tanganyika cichlids, relevant available sequences of Ergasilidae from 5 genera were retrieved from GenBank (for details, see Table 2). Three species of the family Lernaeidae, *Lernaea cyprinacea* (Linnaeus, 1758), *Lamproglena chinensis* (Yü, 1937) and *Lamproglena orientalis* (Markevich, 1936) were selected as outgroup. Partial sequences of 18S rDNA and 28S rDNA were aligned separately using MAFFT v.7 (Katoh and Standley, 2013), applying the G-INS-i iterative refinement algorithm. Gaps and ambiguously aligned regions were removed from the alignments with Gblocks v0.91b (Talavera and Castresana, 2007) using settings for a less stringent selection. jModelTest 2.1.10 (Darriba *et al.*, 2012) was employed to select the most appropriate model of DNA evolution, using the Bayesian information criterion for each individual gene. The most suitable evolutionary model was TIM3e + I + G for the partial gene encoding 18S rRNA and TIM3 + F + I + G for the partial gene of 28S rRNA. The final phylogenetic reconstruction was performed on the concatenated dataset including partial 18S rDNA (991 bp) and partial 28S rDNA (588 bp) using maximum likelihood (ML) and Bayesian inference (BI) methods. ML analyses were carried out using IQ-TREE (Nguyen *et al.*, 2015) on the W-IQ-TREE webserver (Trifinopoulos *et al.*, 2016) and nodal support for the tree was assessed through ultrafast bootstrap approximation with 1000 replicates (Hoang *et al.*, 2018). BI analysis was run in MrBayes 3.2.6 (Huelsenbeck and Ronquist, 2001) using the CIPRES platform (Miller *et al.*, 2010), by setting the GTR + F + I (nst = 6 rates = invgamma) model for each partition; the analysis included 2 simultaneous runs of Markov chain Monte Carlo for 10 000 generations, sampling every 100 generations, with a 'burn-in' of 25%. The results were checked in Tracer v. 1.7.1 (Rambaut *et al.*, 2018) to assess chain convergence. The trees were visualized and edited in FigTree v1.4.3 (Rambaut, 2012). Genetic distances (uncorrected *p*-distance) were calculated in MEGA v.11 (Tamura *et al.*, 2021).

Results

The gill-associated parasitic copepods were obtained from 12 species of cichlids inhabiting Lake Tanganyika. All specimens were assigned to *Ergasilus* on the basis of several diagnostic characters, according to Boxshall and Montú (1997); Boxshall and Halsey (2004); Suárez-Morales and Santana-Piñeros (2008). These included (i) biramous leg IV with 2-segmented exopod and 3-segmented endopod, (ii) 6-segmented antennule, (iii) antenna with a single claw and (iv) the absence of maxillipeds in females. Three new and 2 previously described species of *Ergasilus* are figured and described below.

Species richness of *Ergasilus* parasites on the host species investigated ranged from 1 to 4. *Bathybates ferox* and *Ctenochromis horei* were each found to harbour 1 *Ergasilus* species (i.e. *E. megacheir* and *E. parvus* n. sp., respectively). *Eretmodus marksmithi* and *Lamprologus callipterus* were each found to be hosts of 4 *Ergasilus* species (i.e. *E. caparti* n. sp., *E. macrodactylus*, *E. parasarsi* n. sp. and *E. parvus* n. sp.). The

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Table 1. List of all sampled fishes and their sampling localities

Host species	Locality name and number	Coordinates
Astatotilapia burtoni (Günther, 1894)	Fish market Bujumbura	3°23′S, 29°22′E
Aulonocranus dewindti (Boulenger, 1899)	Magara, Lake Tanganyika, Burundi (1)	3°44′S, 29°19′E
***Bathybates ferox* (Boulenger, 1898)**	Nyaruhongoka, Lake Tanganyika, Burundi (4)	3°41′S, 29°20′E
Bathybates graueri (Steindachner, 1911)	Fish market Bujumbura*	3°23′S, 29°22′E
Bathybates minor (Boulenger, 1906)	Fish market Bujumbura	3°23′S, 29°22′E
Benthochromis tricoti (Poll, 1948)	Fish market Bujumbura	3°23′S, 29°22′E
Boulengerochromis microlepis (Boulenger, 1899)	Fish market Bujumbura	3°23′S, 29°22′E
Cyprichromis microlepidotus (Poll, 1956)	Fish market Bujumbura	3°23′S, 29°22′E
	Nyaruhongoka, Lake Tanganyika, Burundi (4)	3°41′S, 29°20′E
***Ctenochromis horei* (Günther, 1894)**	Fish market Bujumbura	3°23′S, 29°22′E
	Magara, Lake Tanganyika, Burundi (1)	3°44′S, 29°19′E
	Mvugo, Lake Tanganyika, Burundi (3)	4°15′S, 29°34′E
	Nyaruhongoka, Lake Tanganyika, Burundi (4)*	3°41′S, 29°20′E
***Eretmodus marksmithi* (Burgess, 2012)**	Magara, Lake Tanganyika, Burundi (1)*	3°44′S, 29°19′E
	Mukuruka, Lake Tanganyika, Burundi (2)*	4°14′S, 29°33′E
	Nyaruhongoka, Lake Tanganyika, Burundi (4)*	3°41′S, 29°20′E
***Gnathochromis permaxillaris* (David, 1936)**	Mukuruka, Lake Tanganyika, Burundi (2)*	4°14′S, 29°33′E
Gnathochromis pfefferi (Boulenger, 1898)	Mvugo, Lake Tanganyika, Burundi (3)	4°15′S, 29°34′E
Hemibates stenosoma (Boulenger, 1901)	Fish market Bujumbura	3°23′S, 29°22′E
***Lamprologus callipterus* (Boulenger, 1906)**	Magara, Lake Tanganyika, Burundi (1)*	3°44′S, 29°19′E
Limnochromis auratus (Boulenger, 1901)	Mukuruka, Lake Tanganyika, Burundi (2)*	4°14′S, 29°33′E
	Nyaruhongoka, Lake Tanganyika, Burundi (4)*	3°41′S, 29°20′E
	Fish market Bujumbura	3°23′S, 29°22′E
***Neolamprologus brichardi* (Poll, 1974)**	Magara, Lake Tanganyika, Burundi (1)*	3°44′S, 29°19′E
	Nyaruhongoka, Lake Tanganyika, Burundi (4)	3°41′S, 29°20′E
***Neolamprologus mondabu* (Boulenger, 1906)**	Mvugo, Lake Tanganyika, Burundi (3)*	4°15′S, 29°34′E
	Nyaruhongoka, Lake Tanganyika, Burundi (4)*	3°41′S, 29°20′E
***Ophthalmotilapia nasuta* (Poll & Matthes, 1962)**	Magara, Lake Tanganyika, Burundi (1)*	3°44′S, 29°19′E
***Perissodus microlepis* (Boulenger, 1898)**	Magara, Lake Tanganyika, Burundi (1)*	3°44′S, 29°19′E
	Nyaruhongoka, Lake Tanganyika, Burundi (4)*	3°41′S, 29°20′E
***Simochromis diagramma* (Günther, 1893)**	Magara, Lake Tanganyika, Burundi (1)*	3°44′S, 29°19′E
	Nyaruhongoka, Lake Tanganyika, Burundi (4)	3°41′S, 29°20′E
***Spathodus erythrodon* (Boulenger, 1900)**	Magara, Lake Tanganyika, Burundi (1)*	3°44′S, 29°19′E
***Tanganicodus irsacae* (Poll, 1950)**	Mukuruka, Lake Tanganyika, Burundi (2)*	4°14′S, 29°33′E
Trematocara unimaculatum (Boulenger, 1901)	Fish market Bujumbura	3°23′S, 29°22′E

Parasitized fishes are highlighted in bold, localities on which the host was parasitized by *Ergasilus* is marked with the symbol*.

number of host species ranged from 2 for *E. megacheir* to a maximum of 7 for *E. parvus* n. sp. (Table 3). The highest prevalence (100%) was observed for *E. macrodactylus* on *Gnathochromis permaxillaris* and *Perissodus microlepis*, as well as for *E. parvus* n. sp. on *B. ferox* (only 1 specimen examined). The highest intensity of infection (62 individuals) was observed for *E. caparti* n. sp. on *E. marksmithi* (for detailed information see Table 3).

Family Ergasilidae (Burmeister, 1835)
Genus *Ergasilus* (von Nordmann, 1832)

***Ergasilus macrodactylus* (Sars, 1909)**
Syn. *Ergasiloides macrodactylus* (Sars, 1909)

Type-host: not recorded.
Type locality: Lake Tanganyika, Sumbu, Zambia.
Site on host: gill filaments.
Other previous records: *Brycinus imberi* (Peters, 1852) (Characiformes: Alestidae), *Haplochromis* spp., *Lethrinops* spp., *Pseudotropheus* spp., *Tilapia* spp. (Cichliformes: Cichlidae), Lake Malawi, Malawi (Fryer, 1956).
Present records: *E. marksmithi* (localities 1, 2, 4); *G. permaxillaris* (locality 2); *L. callipterus* (localities 2, 4); *P. microlepis* (locality 4); *Tanganicodus irsacae* (locality 2) (see Table 1).
Comparative material examined: four voucher specimens of *E. macrodactylus* (Sars, 1909) from *Haplochromis* spp. (Malawi): RBINS COP 6086, 6087, 6088 and 6089.

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Table 2. List of parasitic copepods used for phylogenetic analysis, including their host species, collection locality and accession numbers for partial 18S and 28S rDNA sequences

Parasite species	Host species	Host family	Locality	GenBank accession numbers		Reference
				18S	28S	
Ergasilidae						
Acusicola margulisae	*Amphilophus citrinellus*	Cichlidae	Nicaragua	MN852694	MN852851	Santacruz *et al.* (2020)
Ergasilus anchoratus	*Tachysurus fulvidraco*	Bagridae	Baoan Lake, China	DQ107564	DQ107528	Song *et al.* (2008)
Ergasilus briani	*Misgurnus anguillicaudatus*	Cobitidae	Dangjiangkou, China	DQ107572	DQ107532	Song *et al.* (2008)
***Ergasilus caparti* n. sp.**	*Neolamprologus brichardi*	Cichlidae	Lake Tanganyika, Burundi	OQ407469	OQ407474	present study
Ergasilus hypomesi	*Acanthogobius hasta*	Gobiidae	Dangjiangkou, China	DQ107573	DQ107539	Song *et al.* (2008)
Ergasilus macrodactylus	*Gnathochromis permaxillaris*	Cichlidae	Lake Tanganyika, Burundi	OQ407465	OQ407470	present study
Ergasilus megacheir	*Simochromis diagramma*	Cichlidae	Lake Tanganyika, Burundi	OQ407466	OQ407471	present study
***Ergasilus parasarsi* n. sp.**	*Simochromis diagramma*	Cichlidae	Lake Tanganyika, Burundi	OQ407467	OQ407473	present study
Ergasilus parasiluri	*Tachysurus fulvidraco*	Bagridae	Dangjiangkou, China	DQ107568	DQ107536	Song *et al.* (2008)
***Ergasilus parvus* n. sp.**	*Spathodus erythrodon*	Cichlidae	Lake Tanganyika, Burundi	OQ407468	OQ407472	present study
Ergasilus peregrinus	*Siniperca chuatsi*	Sinipercidae	Dangjiangkou, China	DQ107577	DQ107531	Song *et al.* (2008)
Ergasilus scalaris	*Tachysurus dumerili*	Bagridae	Poyang Lake, China	DQ107565	DQ107538	Song *et al.* (2008)
Ergasilus sieboldi	*Perca fluviatilis*	Percidae	U Jezu, Czech Republic	MW810238	MW810242	Kvach *et al.* (2021)
Ergasilus tumidus	*Acheilognathus taenianalis*	Acheilognathidae	Niushan Lake, China	DQ107569	DQ107535	Song *et al.* (2008)
Ergasilus wilsoni	–	–	South Korea	KR048765	KR048843	Baek *et al.* (2016)
Ergasilus yaluzangbus	*Oxygymnocypris stewartii*	Cyprinidae	Lasa River, Tibet	DQ107578	DQ107540	Song *et al.* (2008)
Neoergasilus japonicus	*Lepomis gibbosus*	Centrarchidae	Rohlík, Czech Republic	MH167970	MH167968	Ondračková *et al.* (2019)
Paraergasilus brevidigitus	*Cyprinus carpio*	Cyprinidae	Tangxun Lake, China	DQ107576	DQ107530	Song *et al.* (2008)
Paraergasilus longidigitus	*Abramis brama*, *Perca fluviatilis*, *Scardinius erythrophthalmus*	Leuciscinae, Percidae,	Pahrbek, U Jezu, Czech Republic	MW810239	MW810243	Kvach *et al.* (2021)
Paraergasilus medius	*Ctenopharyngodon idella*	Xenocyprididae	Tangxun Lake, China	DQ107574	DQ107529	Song *et al.* (2008)
Sinergasilus major	*Ctenopharyngodon idella*	Xenocyprididae	Tangxun Lake, China	DQ107558	DQ107524	Song *et al.* (2008)
Sinergasilus polycolpus	*Hypophthalmichthys molitrix*	Xenocyprididae	Tangxun Lake, China	DQ107563	DQ107525	Song *et al.* (2008)
Sinergasilus undulatus	*Cyprinus carpio*	Cyprinidae	Tangxun Lake, China	DQ107561	DQ107526	Song *et al.* (2008)
Lernaeidae						
Lamproglena chinensis	*Channa argus*	Channidae	Dangjiangkou, China	DQ107553	DQ107545	Song *et al.* (2008)
Lamproglena orientalis	*Chanodichthys dabryi*	Xenocyprididae	Tangxun Lake, China	DQ107549	DQ107542	Song *et al.* (2008)
Lernaea cyprinacea	*Chanodichthys erythropterus*	Xenocyprididae	Dongxi Lake, China	DQ107555	DQ107547	Song *et al.* (2008)

Newly generated sequences are given in bold.

Table 3. Prevalence (first line), mean intensity of infection (second line) and intensity of infection (min–max; third line) of 5 *Ergasilus* species from Lake Tanganyika found on 12 cichlid host species (n = total number of host specimens examined)

Parasite species	*B. ferox* (n = 1)	*C. horei* (n = 11)	*E. marksmithi* (n = 28)	*G. permaxillaris* (n = 10)	*L. callipterus* (n = 15)	*N. brichardi* (n = 12)	*N. mondabu* (n = 17)	*O. nasuta* (n = 3)	*P. microlepis* (n = 5)	*S. diagramma* (n = 11)	*S. erythrodon* (n = 9)	*T. irsacae* (n = 7)
Ergasilus macrodactylus	–	–	17.8 15.8 (3–38)	100 8.5 (2–16)	60 8.4 (2–15)	–	–	–	100 6.4 (2–13)	–	–	57.1 15.5 (5–28)
Ergasilus megacheir	–	9.1 1 (1)	–	–	–	–	–	–	–	36.3 2.5 (2–4)	–	–
Ergasilus caparti n. sp.	–	–	50 21.2 (2–62)	–	6.6 1 (1)	8.3 4 (4)	50 3.5 (1–9)	–	–	–	11.1 22 (22)	–
Ergasilus parasarsi n. sp.	–	–	3.6 8 (8)	–	6.6 15 (15)	–	–	66.6 6.5 (6–7)	–	9.1 27 (27)	33.3 13.3 (4–24)	42.9 7 (5–9)
Ergasilus parvus n. sp.	100 18 (18)	–	32.1 28.5 (11–61)	–	20 11.6 (1–20)	50 1.6 (1–3)	17.6 3 (1–5)	–	–	36.3 5.5 (1–12)	77.7 8.9 (2–19)	–

Voucher material deposited: Cr-33 (2 specimens, locality 2); hologenophore: Cr-33 (3 specimens, locality 2).

Representative DNA sequences: 18S rDNA (GenBank acc. no. OQ407465) and 28S rDNA (GenBank acc. no. OQ407470) (see also Table 2) sequences from 5 specimens ex *E. marksmithi* (n = 1), *G. permaxillaris* (n = 3) and *P. microlepis* (n = 1).

Description

Adult female [based on 10 specimens; Figs 2 and 3]. Body length (measured from anterior margin of prosome to posterior margin of caudal rami) 659 (554–864; n = 10). Body comprising prosome and urosome (Fig. 2A). Prosome 5-segmented, composed of cephalosome and 4 pedigerous somites; cephalosome and first pedigerous somite separate.

Cephalosome trapezoidal, with truncate frontal margin and distinctly projecting postero-lateral corners; antennules and antennae visible in dorsal view. Cephalic ornamentation comprising anterior and posterior circular markings of similar sizes; an inverted T-structure of thickened chitin situated postmedially on dorsal side. Eye spot clearly visible near anterior margin of cephalosome. Four pedigerous somites evenly rounded at lateral margins, decreasing in length and width posteriorly.

Urosome narrow, comprising short fifth pedigerous somite, genital segment (Fig. 2F), and 3 free abdominal somites. Genital segment barrel-shaped, posteriorly tapered, with dorsal bilateral cuticular ornamentation. Abdominal somites slightly decreasing in width posteriorly; third abdominal somite slightly incised medially.

Caudal rami with subrectangular shape, slightly longer than wide, posteriorly widening; each ramus armed with 4 terminal setae – the innermost furcal seta at least 5 times longer than others, slightly swollen near the basis and directed outwards. Two egg sacs (Fig. 2G), much longer than wide; each composed of 2–3 rows of circular-shaped eggs and reaching beyond the longest furcal setae.

Antennule (Fig. 2E) 6-segmented; segments well defined and tapering distally, armed with simple setae; setal formula from proximal to distal segments: 4–7–6–3–2–4.

Antenna (Fig. 2B) comprising short coxobasis, 3-segmented endopod and curved terminal claw. First endopod segment twice as long as the coxobasis and attenuated distally; no hyaline border present. Second endopod segment elongated, slightly corrugated in its proximal third. Third endopodal segment small. Terminal claw very slender, pointed and smooth. Antenna without setules or spines.

Mouthparts comprising mandible, maxillule and maxilla; maxilliped absent. Mandible consisting of 3 blades (anterior, middle and posterior); each blade with small teeth on anterior margin (Fig. 2C). Maxillule a small single lobe, with 2 almost equally long distal setae. Maxilla 2-segmented, with numerous sharp teeth on anterior margin of distal segment (Fig. 2D).

Swimming legs I to IV; each comprising coxa, basis and 2 segmented rami (i.e. exopod, endopod) (Fig. 3). Rami of all legs 3-segmented, except 2-segmented exopod of leg IV. Segments distinct, typical of members of the genus. Interpodal plates of all legs lacking spinules. Armature on rami as follows (Roman and Arabic numerals indicating spines and plumose setae, respectively) in Table 4.

Leg I (Fig. 3A) coxa unarmed, basis with outer seta. Exopod 3-segmented; first segment with small outer spine; second segment with inner plumose seta and a small outer spine; third segment with small spine on outer corner, longer apical spine and 5 plumose setae. Endopod 3-segmented; first and second segment each with 1 plumose seta; third segment with 4 plumose setae and 2 distal spines.

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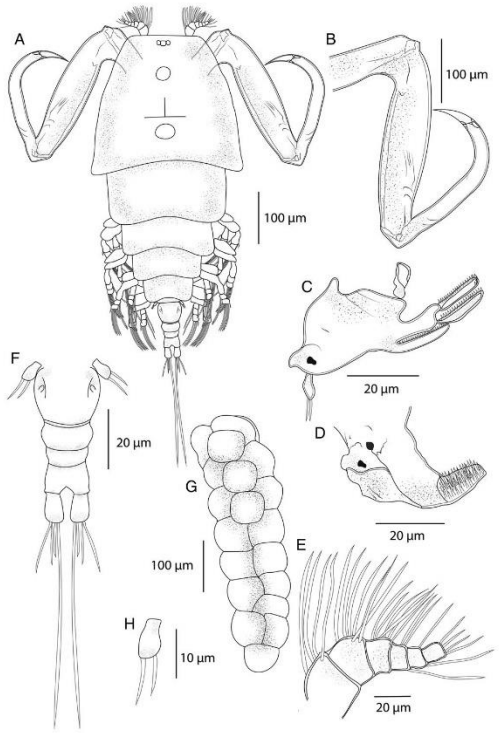


Fig. 2. *Ergasilus macrodactylus*, adult female from *Gnathochromis permaxillaris*. (A) Habitus, dorsal; (B) antenna, ventral; (C) mandible and maxilulle, ventral; (D) maxilla, ventral; (E) antennule, ventral; (F) abdomen and caudal rami; (G) egg sac, dorsal; (H) leg V, ventral.

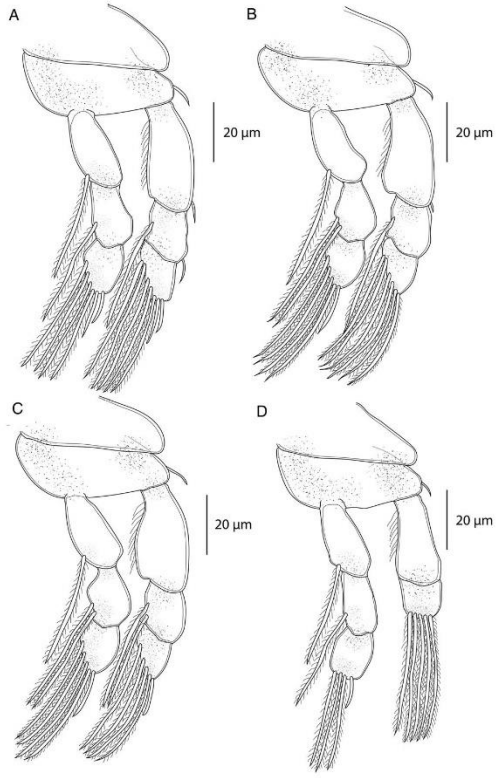


Fig. 3. *Ergasilus macrodactylus*, adult female from *Gnathochromis permaxillaris*. (A) Leg I, ventral; (B) leg II, ventral; (C) leg III, ventral; (D) leg IV, ventral.

Leg II (Fig. 3B) coxa unarmed, basis with outer seta. Exopod 3-segmented; first segment with very small outer spine; second segment with 1 plumose seta, lacking spine; third segment with 6 plumose setae. Endopod 3-segmented; first segment with 1 plumose seta; second segment with 2 plumose setae; third segment with 4 plumose setae and 1 distal spine.

Leg III (Fig. 3C) coxa unarmed, basis with outer seta. Exopod 3-segmented; first segment lacking armature; second segment with 2 plumose setae; third segment with 4 plumose setae and 1 distal spine. Endopod 3-segmented; first segment with 1 plumose seta; second segment with 2 plumose setae; third segment with 4 plumose setae and 1 distal spine.

Leg IV (Fig. 3D) coxa unarmed, basis with outer seta. Exopod 2-segmented; first segment longest and without armature; second segment with 5 plumose setae. Endopod 3-segmented; first and second segment each with 1 plumose seta; third segment with 3 plumose setae and 1 distal spine.

Leg V (Fig. 2H) simple and visible, with cylindrical form, bearing 2 terminal simple seta.

Specimens preserved in ethanol rather light in colour; traces of a purple pigment in cephalothorax observed after clearing in lactic acid.

Male: unknown.

Remarks

Ergasilus macrodactylus is characterized, in part, by having trapezoidal cephalothorax, elongate antenna and clearly visible eye spot (Fryer, 1956). Based on the overall body shape, this species is similar to *E. megacheir* but clearly differs from it by having: (i) 3-segmented abdomen; (ii) the first endopod segment of the antenna without hyaline border on anterior edge; (iii) elongate and distally recurved second endopod segment of the antenna (second endopod segment short and twisted in *E. megacheir*); (iv) the terminal claw of the antenna with smooth margins (claw with inner denticle in *E. megacheir*); (v) a tiny spine on the first segment of the exopod of leg II; (vi) 2 plumose setae on the second segment of the endopods of leg II and III (1 plumose seta on the respective endopods in *E. megacheir*); and (vii) a different spine–seta formula on the exopod of leg III (0–0, 0–2, I–4 *vs* 0–0, 0–1, 0–6 in *E. megacheir*).

Ergasilus macrodactylus was a cause of much confusion in the past. This species has been described as *Ergasiloides macrodactylus* (Sars, 1909), and later transferred to *Ergasilus* by Fryer

Table 4. Spine and setal formula of swimming legs of *E. macrodactylus*

	Coxa	Basis	Exopod	Endopod
Leg I	0–0	1–0	I–0; I–1; II–5	0–1; 0–1; II–4
Leg II	0–0	1–0	I–0; 0–1; 0–6	0–1; 0–2; I–4
Leg III	0–0	1–0	0–0; 0–2; I–4	0–1; 0–2; I–4
Leg IV	0–0	1–0	0–0; 0–5	0–1; 0–1; I–3

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(1956), when he found specimens conspecific with *E. macrodactylus* in Lake Malawi. According to Fryer (1956), Sars (1909) was wrong when he based the description of his species on immature specimens, and therefore wrongly placed it in *Ergasiloides*. Although *E. macrodactylus* was already reported in Lake Tanganyika by Sars (1909), it was omitted from the checklist for parasites from Lake Tanganyika (Avenant-Oldewage and Oldewage, 1993). Our findings confirm the presence of *E. macrodactylus* in Lake Tanganyika, even though the overall body size of our specimens is slightly smaller than those of Fryer (1956) (i.e. 659 *vs* 765). In this respect, our specimens of *E. macrodactylus* are more similar to those of Sars (1909).

***Ergasilus megacheir* (Sars, 1909)**
Syn. *Ergasiloides megacheir* (Sars, 1909)
Type-host: not recorded.
Type-locality: Lake Tanganyika, Sumbu, Zambia.
Site on host: gill filaments.
Other previous records: *Pterochromis congicus* (Boulenger, 1897) (Cichliformes: Cichlidae), Lake Tumba, Congo System (Fryer, 1964); *Bathybates minor* (Boulenger, 1906), *Bathybates fasciatus* (Boulenger, 1901), *Cyphotilapia frontosa* (Boulenger, 1906), *Haplotaxodon microlepis* (Boulenger, 1906), *Limnotilapia dardenii* (Boulenger, 1899), *Pseudosimochromis curvifrons* (Poll, 1942) (Cichliformes: Cichlidae), *Synodontis multipunctatus* (Boulenger, 1898), *Synodontis granulosus* (Boulenger, 1900) (Siluriformes: Mochokidae), Lake Tanganyika (Fryer, 1965); *Simochromis* sp. (Cichliformes: Cichlidae), Lake Tanganyika (Capart, 1944); unknown hosts, Lake Tanganyika (Sars, 1909; Cunnington, 1920).
Present records: ex *C. horei* (locality 4); *Simochromis diagramma* (locality 1) (see Table 1).
Voucher material deposited: Cr-34 (1 specimen, locality 1); hologenophore: Cr-34 (1 specimen, locality 1).
Representative DNA sequences: 18S rDNA (GenBank acc. no. OQ407466) and 28S rDNA (GenBank acc. no. OQ407471) (see also Table 2) sequences from 2 specimens ex *S. diagramma*.

Description

Adult female [based on 5 specimens; Figs 4 and 5]. Body length (measured from anterior margin of prosome to posterior margin of caudal rami) 698 (613–770; $n = 5$). Prosome 5-segmented, composed of cephalosome and 4 pedigerous somites; cephalosome and first pedigerous somite separate (Fig. 4A). Cephalosome quadrangular, frontal edge truncated, postero-lateral corners slightly prominent and rounded; antennules and antennae visible in dorsal view. Cephalic ornamentation comprising anterior ovoid marking and posterior oval marking; an inverted T-structure of thickened chitin situated postmedially on dorsal side, between the circular and oval marking. Eye spot clearly visible near anterior margin of cephalosome. Four pedigerous somites with lateral parts slightly produced backwards, rounded obtusely at the end.

Urosome small, comprising short fifth pedigerous somite, genital segment (Fig. 4F) and 2 free abdominal somites. Fifth pedigerous somite almost wholly concealed. Genital segment barrel-shaped, anteriorly tapered.

Second abdominal somite shallowly incised medially, much longer than preceding somite. Caudal rami subrectangular, as long as the length of the previous segment; each ramus armed with 4 terminal setae – the innermost longest and thickest; outer setae pointing towards middle body axis.

Two egg sacs (Fig. 4G) much longer than wide; each composed of 2–4 rows of circular-shaped eggs. Some specimen egg sacs extremely long, almost the same length as the whole body.

Antennule (Fig. 4E) 6-segmented; segments well defined, tapering distally, armed with simple setae; setal formula from proximal to distal segments: 4–11–3–4–3–6.

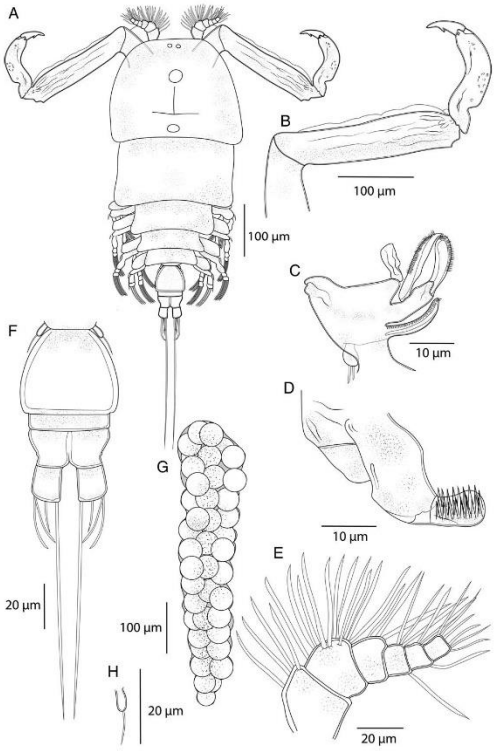


Fig. 4. *Ergasilus megacheir*, adult female from *Simochromis diagramma*. (A) Habitus, dorsal; (B) antenna, ventral; (C) mandible and maxilulle, ventral; (D) maxilla, ventral; (E) antennule, ventral; (F) abdomen and caudal rami; (G) egg sac, dorsal; (H) leg V, ventral.

Antenna (Fig. 4B) comprising short coxobasis, 3-segmented endopod, and strongly curved terminal claw. First endopodal segment twice as long as the coxobasis, oblong in form, distally slightly narrowed; anterior edge with visible thin hyaline border not fully extending to the base. Second endopodal segment short and twisted, third endopodal segment inconspicuous. Terminal claw about 1/3 length of second endopodal segment, equipped with a recurved denticle inside. Antenna without setules or spines.

Mouthparts comprising mandible, maxillule and maxilla; maxilliped absent. Mandible consisting of 3 blades (anterior, middle and posterior); each blade with small sharp teeth; anterior and posterior blade with teeth located on anterior margin; middle blade with teeth on posterior margin (Fig. 4C). Maxilulle a small lobe with 2 unequally long distal setae and 2 minute inner setae. Maxilla 2-segmented, comprising unarmed syncoxa and basis, distally with numerous sharp teeth on anterior margin (Fig. 4D).

Swimming legs I–IV; each comprising coxa, basis and 2 segmented rami (i.e. exopod, endopod) (Fig. 5). Rami of all legs 3-segmented, except 2-segmented exopod of leg IV. Segments distinct, typical of members of the genus. Interpodal plates of all legs lacking spinules. Armature on rami as follows (Roman and Arabic numerals indicating spines and setae, respectively) in Table 5.

Leg I (Fig. 5A) coxa unarmed, basis with proximal outer seta. Exopod 3-segmented; first segment with small outer spine; second segment with inner plumose seta and a small outer spine; third

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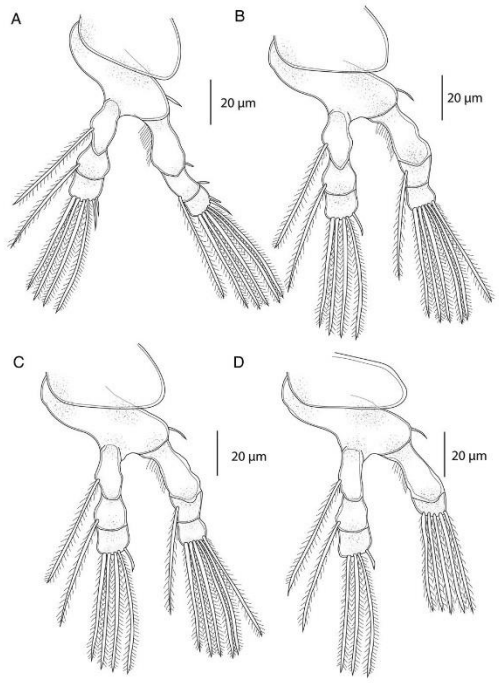


Fig. 5. *Ergasilus megacheir*, adult female from *Simochromis diagramma*. (A) Leg I, ventral; (B) leg II, ventral; (C) leg III, ventral; (D) leg IV, ventral.

Table 5. Spine and setal formula of swimming legs of *E. megacheir*

	Coxa	Basis	Exopod	Endopod
Leg I	0–0	1–0	I–0; I–1; II–5	0–1; 0–1; II–4
Leg II	0–0	1–0	0–0; 0–1; 0–6	0–1; 0–1; I–4
Leg III	0–0	1–0	0–0; 0–1; 0–6	0–1; 0–1; I–4
Leg IV	0–0	1–0	0–0; 0–5	0–1; 0–1; I–3

segment with small spine on outer corner, longer apical spine and 5 plumose setae. Endopod 3-segmented; first and second segment each with 1 plumose seta; third segment with small spine on outer corner, longer distal spine and 4 plumose setae.

Legs II and III (Fig. 5B and C) similar. Coxa unarmed, basis with proximal outer seta. Exopod with 3 segments; first segment lacking armature; second segment with 1 plumose seta, lacking spine; third segment with 6 plumose setae. Endopod with 3 segments; first and second segment each with 1 plumose seta; third segment with 4 plumose setae and 1 distal spine.

Leg IV (Fig. 5D) coxa unarmed, basis with proximal outer seta. Exopod 2-segmented; first segment longest without armature; second segment with 5 plumose setae. Endopod with 3 segments; first and second segment each with 1 plumose seta; third segment with 3 plumose setae and 1 distal spine.

Leg V (Fig. 4H) extremely small, barely visible, with 1 smooth seta.

Specimens preserved in ethanol brown in colour. No pigment observed after clearing in lactic acid.

Male: unknown.

Remarks

Ergasilus megacheir was already recorded from Lake Tanganyika by Sars (1909), Cunnington (1920), Capart (1944) and Fryer (1965). Fryer (1964) reported this species also from Lake Tumba in Lower Congo. *Ergasilus megacheir* is easily distinguished from other congeners by the presence of a denticle on the inner side of the terminal claw of the antenna. The size of the denticle differs, being more prominent in presumably smaller specimens and less visible in bigger specimens, which supports Fryer's (1965) previous observation. Based on comparative morphology, *E. megacheir* is most similar to *E. macrodactylus*. The differentiation of both species is provided in the remarks for the latter species.

Although *E. megacheir* was the least abundant species in our dataset, its presence in the Lake was reconfirmed after more than 50 year. For the first time, egg sacs were described and drawn. The presence of setae on the basis of legs I–IV was also confirmed. The spine can be seen in the original drawings but did not feature in the spine–seta formula.

***Ergasilus caparti* n. sp.**

Type-host: *Neolamprologus brichardi* (Poll, 1974).

Type-locality: Magara (3°44′S, 29°19′E), Lake Tanganyika, Burundi.

Other hosts and localities: *E. marksmithi* (localities 1, 2), *L. callipterus* (locality 4), *Neolamprologus mondabu* (locality 3), *P. microlepis* (locality 1), *Spathodus erythrodon* (locality 1) (see Table 1).

Type and voucher material: holotype (adult female): (Cr-35) ex *N. brichardi*; paratypes (adult females): Cr-35 ex *E. marksmithi*; hologenophores (adult females): Cr-35 ex *S. erythrodon* and *E. marksmithi*.

Site on host: gill filaments.

ZooBank registration: urn:lsid:zoobank.org:act:7211AE50-81DA-4F73-BE5E-26611C2974C4

Representative DNA sequences: 18S rDNA (GenBank acc. no. OQ407469) and 28S rDNA (GenBank acc. no. OQ407474) (see also Table 2) sequences from 5 specimens ex *E. marksmithi* ($n = 1$), *L. callipterus* ($n = 1$), *N. mondabu* ($n = 1$) and *S. erythrodon* ($n = 2$).

Etymology: This species is named after André Capart (1917–1993), director of the Royal Institute of Natural Sciences (Belgium), to honour his contributions to knowledge of the crustacean fauna that resulted from expeditions to the African Great Lakes including Lake Tanganyika (1946–1947).

Description

Adult female [based on 10 specimens; Figs 6 and 7]. Body length (measured from anterior margin of prosome to posterior margin of caudal rami) 509 (411–611; $n = 10$). Prosome 5-segmented, composed of cephalosome and 4 pedigerous somites; cephalosome and first pedigerous somite separate. Cephalosome hexagonal, with a medial indentation on posterior margin; antennules and antennae visible in dorsal view (Fig. 6A). Cephalic ornamentation comprising anterior circular marking and a more posterior, slightly larger oval marking; an inverted T-structure of thickened chitin situated medially on dorsal side, between the circular and oval marking. First pedigerous somite of similar size as cephalosome, slightly tapering medially. Second to fourth pedigerous somites each markedly narrowing posteriorly.

Urosome comprising short fifth pedigerous somite, genital segment (Fig. 6F), and 2 free abdominal somites. Genital segment of similar shape to the first pedigerous somite, slightly widening in posterior half, ventral surface ornate with spinules along postero-ventral margin. Two free abdominal somites with a row of acute spinules along posterior margin on ventral surface.

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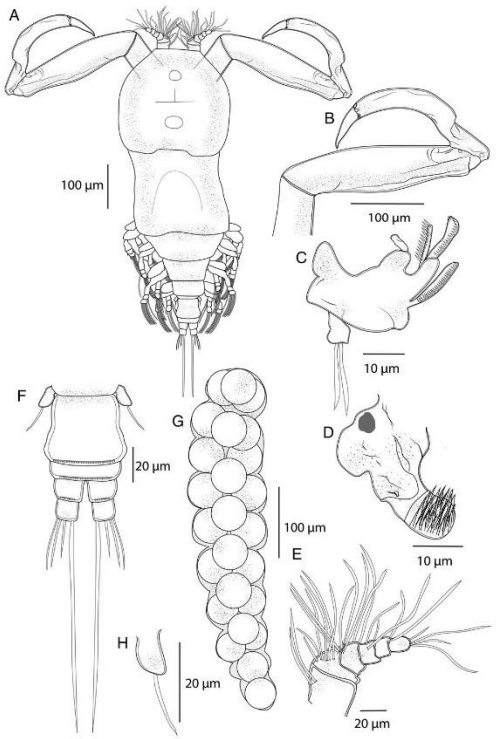


Fig. 6. *Ergasilus caparti* n. sp., adult female from *Neolamprologus brichardi*. (A) Habitus, dorsal; (B) antenna, ventral; (C) mandible and maxilulle, ventral; (D) maxilla, ventral; (E) antennule, ventral; (F) abdomen and caudal rami; (G) egg sac, dorsal; (H) leg V, ventral.

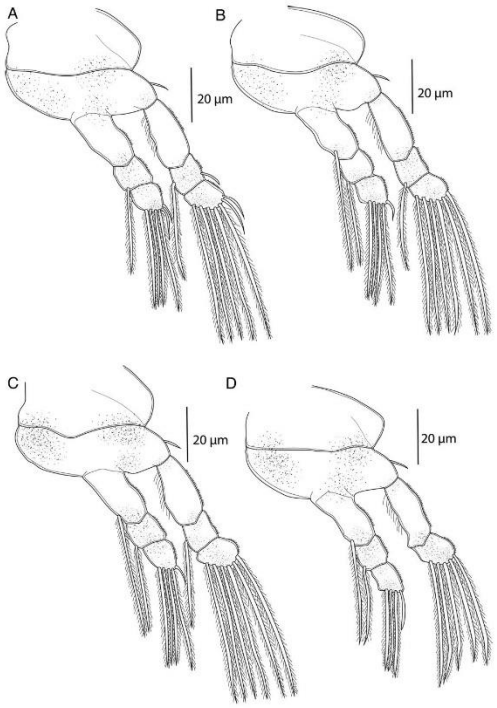


Fig. 7. *Ergasilus caparti* n. sp., adult female from *Neolamprologus brichardi*. (A) Leg I, ventral; (B) leg II, ventral; (C) leg III, ventral; (D) leg IV, ventral.

First abdominal somite short, slightly longer than the fifth pedigerous somite. Second abdominal somite deeply incised medially, slightly larger than the preceding somite.

Caudal rami subrectangular, slightly longer than wide; each ramus bearing 4 terminal setae – the innermost longest and thickest but not exceeding egg sacs. Two egg sacs (Fig. 6G) quite long and narrowing distally; each composed of 2–4 rows of eggs.

Antennule (Fig. 6E) 6-segmented, tapering distally, armed with simple setae; setal formula from proximal to distal segments: 2–10–3–3–2–4.

Antenna (Fig. 6B) comprising short coxobasis, 3-segmented endopod and strongly curved terminal claw. First endopodal segment longest; second endopodal segment proximally with conspicuous indentation of cuticle on outer side, formed by 2 ridges crossing each other. Third endopodal segment small, but more conspicuous under the light microscope than in other species from Lake Tanganyika. Terminal claw about 1/3 length of the second endopodal segment. Antenna without setules or spines.

Mouthparts (Fig. 6C and D) comprising mandible, maxilulle and maxilla; maxilliped absent. Mandible consisting of 3 blades (anterior, middle and posterior); anterior blade with sharp teeth on anterior margin; middle and posterior blade with teeth along posterior margin. Maxilulle a well-developed lobe, bearing 2 almost equally long smooth setae. Maxilla 2-segmented, comprising unarmed syncoxa and basis, distally with numerous sharp teeth on anterior margin.

Swimming legs I–IV; each comprising coxa, basis and 2 segmented rami (i.e. exopod, endopod) (Fig. 7). Rami of all legs 3-segmented, except 2-segmented exopod of leg IV. Segments distinct, typical of members of the genus. Interpodal plates of all legs lacking spinules. Armature on rami as follows (Roman and Arabic numerals indicating spines and setae, respectively) in Table 6.

Leg I (Fig. 7A) coxa unarmed, basis with proximal outer seta. Exopod 3-segmented; first segment lacking armature; second segment with inner plumose seta and a small outer spine; third segment with small spine on outer corner, longer apical spine and 5 plumose setae. Endopod 3-segmented; first segment lacking armature; second segment with 1 plumose seta; third segment with 4 plumose setae and 2 distal spines. Outer margins of both rami partly or completely covered with rows of spinules.

Legs II and III similar (Fig. 7B and C). Coxa unarmed, basis with proximal outer seta. Exopod 3-segmented; first segment lacking armature; second segment with 1 plumose seta, lacking spine; third segment with 6 plumose setae. Endopod

Table 6. Spine and setal formula of swimming legs of *E. caparti* n. sp.

	Coxa	Basis	Exopod	Endopod
Leg I	0–0	1–0	0–0; I–1; II–5	0–0; 0–1; II–4
Leg II	0–0	1–0	0–0; 0–1; 0–6	0–1; 0–1; I–4
Leg III	0–0	1–0	0–0; 0–1; 0–6	0–1; 0–1; I–4
Leg IV	0–0	1–0	0–0; 0–5	0–1; 0–1; I–3

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3-segmented; first and second segment each with 1 plumose seta; third segment with 4 plumose setae and 1 distal spine. Outer margins of both rami partly or completely covered with rows of spinules.

Leg IV (Fig. 7D) coxa unarmed, basis with proximal outer seta. Exopod 2-segmented; first segment longest without armature; second segment with 5 plumose setae. Endopod 3-segmented; first and second segment each with 1 plumose seta; third segment with 3 plumose setae and 1 distal spine. Outer margins of both rami partly or completely covered with rows of spinules.

Leg V (Fig. 6H) reduced but visible, bearing 1 simple seta.

Specimens preserved in ethanol faint brown in colour, sometimes with dark brown spots in the cephalothorax.

Male: unknown.

Remarks

Ergasilus caparti n. sp. shows greatest similarity to *E. cunningtoni* (Capart, 1944), a widely distributed copepod reported from fishes of many families, namely Alestidae, Cichlidae, Clupeidae, Cyprinidae, Distichodontidae, Mochokidae, Mormyridae (*Campylomormyrus elephas* – type host species) and Schilbeidae, from the Congo River System (Capart, 1944; Fryer, 1964, 1967), the Galma River (Shotter, 1977) and Lake Volta (Paperna, 1969). In both species, the second endopodal segment of antenna has a conspicuous indentation of cuticle on outer side, formed by 2 ridges crossing each other. *Ergasilus caparti* n. sp. is differentiated from *E. cunningtoni* by: (i) having a much smaller body size (509 *vs* 970); (ii) having 2-segmented abdomen (*vs* 3-segmented abdomen in *E. cunningtoni*); (iii) the presence of a spine on the basis of legs III and IV; (iv) the absence of a spine on the first segment of the exopod of leg I; (v) the absence of seta on the first segment of endopod of leg I; (vi) the absence of a spine on the first segment of exopods of legs II and III; (vii) having only 1 seta on the second segments of the endopods of legs II, III and IV (*vs* 2 setae in *E. cunningtoni*); (viii) having a less prominent eyespot; (ix) the presence of spinules on the outer margins of both rami of all legs (*vs* both rami of all legs with smooth margins in *E. cunningtoni*).

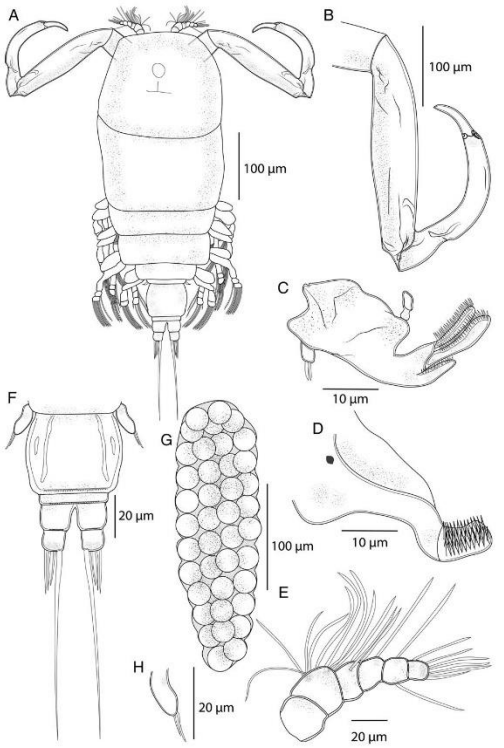


Fig. 8. *Ergasilus parasarsi* n. sp., adult female from *Simochromis diagramma*. (A) Habitus, dorsal; (B) antenna, ventral; (C) mandible and maxilulle, ventral; (D) maxilla, ventral; (E) antennule, ventral; (F) abdomen and caudal rami; (G) egg sac, dorsal; (H) leg V, ventral.

***Ergasilus parasarsi* n. sp.**

Type-host: *S. diagramma* (Günther, 1894)

Type-locality: Magara (3°44′S, 29°19′E), Lake Tanganyika, Burundi.

Other hosts and localities: *E. marksmithi* (locality 1), *G. permaxillaris* (locality 2), *L. callipterus* (locality 2), *Ophthalmotilapia nasuta* (locality 1), *P. microlepis* (locality 4), *T. irsacae* (locality 2) (see Table 1).

Type and voucher material: holotype (adult female): (Cr-36) ex *S. diagramma*; paratypes (adult females): Cr-36 ex *T. irsacae*; hologenophores (adult females): Cr-36 ex *O. nasuta* and *T. irsacae*.

Site on host: gill filaments.

Zoobank registration: urn:lsid:zoobank.org:act:E915E962-E162-4331-BB72-4CE17ADFE5E5

Representative DNA sequences: 18S rDNA (GenBank acc. no. OQ407467) and 28S rDNA (GenBank acc. no. OQ407473) (see also Table 2) sequences from 4 specimens ex *L. callipterus* (n = 2), *O. nasuta* (n = 1) and *T. irsacae* (n = 1).

Etymology: The specific name reflects the close morphological resemblance of the new species to *E. sarsi* (Capart, 1944).

Description

Adult female [based on 10 specimens; Figs 8 and 9]. Body length (measured from anterior margin of prosome to posterior margin of caudal rami) 575 (455–694; n = 10). Body comprising prosome and urosome (Fig. 8A). Prosome 5-segmented, consisting of cephalosome and 4 pedigerous somites; cephalosome and first pedigerous somite separate.

Cephalosome slightly longer than wide, oval to trapezoidal, with antennules and antennae visible in dorsal view. Cephalic ornamentation comprising anterior circular marking and an inverted T-structure of thickened chitin situated medially on dorsal side. First pedigerous somite almost the same length as cephalosome; the other 3 pedigerous somites markedly shorter than the first one, decreasing in length and width posteriorly. Urosome comprising short fifth pedigerous somite, barrel-shaped genital segment (Fig. 8F) and 2 free abdominal somites. Genital segment with dorsal bilateral marking in the form of a stripe running lengthwise and a more laterally situated elongate spot, ventral surface ornate with spinules along postero-ventral margin. Two free abdominal somites with a row of acute spinules along posterior margin on ventral surface. First abdominal somite of similar length as the fifth pedigerous somite. Second abdominal somite deeply incised medially, much larger than the preceding somite. Caudal rami subrectangular, slightly wider than long; each ramus bearing 4 terminal setae – the innermost longest and thickest. Two cylindrical egg sacs (Fig. 8G) relatively short, not exceeding the longest furcal seta.

Antennule (Fig. 8E) 6-segmented, tapering distally, armed with simple setae; setal formula from proximal to distal segments: 0–8–3–1–2–6.

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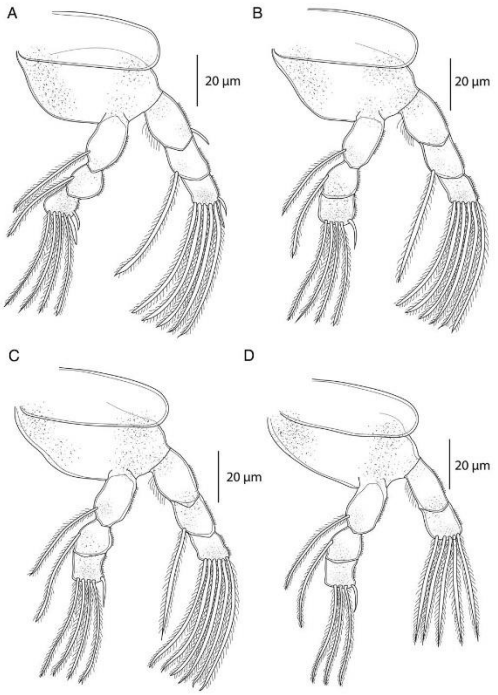


Fig. 9. *Ergasilus parasarsi* n. sp., adult female from *Simochromis diagramma*. (A) Leg I, ventral; (B) leg II, ventral; (C) leg III, ventral; (D) leg IV, ventral.

Antenna (Fig. 8B) prehensile, comprising short coxobasis, 3-segmented endopod and strongly curved terminal claw. First endopodal segment longest; second endopodal segment proximally with indentation of cuticle on outer side; third endopodal segment inconspicuous. Terminal claw about 1/4 length of second endopodal segment. Antenna without setules or spines.

Mouthparts (Fig. 8C and D) comprising mandible, maxillule and maxilla; maxilliped absent. Mandible consisting of 3 blades (anterior, middle and posterior); each blade with sharp teeth on anterior margin. Maxillule a single small lobe, bearing 2 almost equally long smooth setae. Maxilla 2-segmented; syncoxa unarmed; basis relatively slender, distally possessing numerous sharp teeth on anterior margin.

Swimming legs I to IV; each comprising coxa, basis and 2 segmented rami (i.e. exopod, endopod) (Fig. 9). Rami of all legs 3-segmented, except 2-segmented exopod of leg IV. Segments distinct, typical of members of the genus. Interpodal plates of all legs lacking spinules. Armature on rami as follows (Roman and Arabic numerals indicating spines and setae, respectively) in Table 7.

Leg I (Fig. 9A) coxa and basis unarmed. Exopod 3-segmented; first segment with small outer spine; second segment with inner plumose seta, lacking spine; third segment with small spine on outer corner, longer apical spine and 5 plumose setae. Endopod 3-segmented; first segment and second segment each with 1 plumose seta, lacking spine; third segment with 4 plumose setae and 2 distal spines. Outer margins of both rami partly or completely covered with rows of spinules.

Legs II and III similar (Fig. 9B and C). Coxa and basis unarmed. Exopod 3-segmented; first segment lacking armature; second segment with 1 plumose seta, lacking spine; third segment with 6 plumose setae. Endopod 3-segmented; first and second segment each with 1 plumose seta; third segment with 4 plumose setae and 1 distal spine. Outer margins of both rami partly or completely covered with rows of spinules.

Leg IV (Fig. 9D) coxa and basis unarmed. Exopod 2-segmented; first segment longest without armature; second segment with 5 plumose setae. Endopod 3-segmented; first and second segment each with 1 plumose seta; third segment with 3 plumose setae and 1 distal spine. Outer margins of both rami partly or completely covered with rows of spinules.

Leg V (Fig. 8H) reduced but visible, bearing 2 simple setae located distally near each other.

Specimens preserved in ethanol rather light in colour. Traces of blue pigment in cephalothorax (i.e. cephalosome plus first pedigerous somite) observed after clearing in lactic acid.

Male: unknown.

Table 7. Spine and setal formula of swimming legs of *E. parasarsi* n. sp.

	Coxa	Basis	Exopod	Endopod
Leg I	0–0	0–0	I–0; 0–1; II–5	0–1; 0–1; II–4
Leg II	0–0	0–0	0–0; 0–1; 0–6	0–1; 0–1; I–4
Leg III	0–0	0–0	0–0; 0–1; 0–6	0–1; 0–1; I–4
Leg IV	0–0	0–0	0–1; 0–5	0–1; 0–1; I–3

Remarks

Ergasilus parasarsi n. sp. resembles *E. sarsi* that was described from the cichlid *Tylochromis mylodon* (Regan, 1920) from Lake Mweru, Congo Basin, DR Congo (Capart, 1944; Fryer, 1968), and also reported from Lake Tanganyika without mentioning of host species (Sars, 1909; Cunnington, 1920; Capart, 1944). It has also been found in Lake Bangwelu (Fryer, 1959), the Volta Basin (Paperna, 1969) and the River Galma in Niger (Shotter, 1977) from fishes of 5 families, namely Cichlidae, Clariidae, Mochokidae, Mormyridae and Poeciliidae. Detailed morphological comparison of our specimens with the type specimens of *E. sarsi* showed their non-conspecificity. *Ergasilus parasarsi* n. sp. differs from *E. sarsi* by the following characters: (i) different proportions of the first and second endopodal segments of the antenna (first segment much longer than second in *E. sarsi*); (ii) presence of a spine on the first segment of the exopod of leg I; (iii) the absence of a spine on the first segment of the exopod of leg IV; (iv) having only 1 seta on the second segment of the exopods of legs II, III and IV (*vs* 2 setae in *E. sarsi*); and (v) the presence of spinules on the outer margins of both rami of all legs (*vs* both rami of all legs with smooth margins in *E. sarsi*).

***Ergasilus parvus* n. sp.**

Type-host: *S. erythrodon* (Boulenger, 1900)

Type-locality: Magara (3°44′S, 29°19′E), Lake Tanganyika, Burundi.

Other hosts and localities: *B. ferox* (fish market in Burundi), *E. marksmithi* (localities 1, 4), *L. callipterus* (locality 1), *N. brichardi* (locality 1), *N. mondabu* (locality 4) (see Table 1).

Type and voucher material: holotype (adult female): (Cr-37) ex *S. erythrodon*; paratype (adult female): (Cr-37) ex *S. erythrodon*; hologenophores (adult females): Cr-37 ex. *S. erythrodon* and *L. callipterus*.

Site on host: gill filaments.

Zoobank registration: urn:lsid:zoobank.org:act:40C5AD22-CF1E-4873-8F58-E0774928E368

Representative DNA sequences: 18S rDNA (GenBank acc. no. OQ407468) and 28S rDNA (GenBank acc. no. OQ407472) (see also Table 2) sequences from 6 specimens ex *B. ferox* ($n = 1$), *E. marksmithi* ($n = 2$), *N. brichardi* ($n = 1$) and *S. erythrodon* ($n = 2$).

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Etymology: The specific name (an adjective) is from Latin (*parvus* = small) and refers to the body size.

Description

Adult female [based on 10 specimens; Figs 10 and 11]. Body length (measured from anterior margin of prosome to posterior margin of caudal rami) 475 (417–533; $n = 10$). Body comprising prosome and urosome (Fig. 10A). Prosome 5-segmented, composed of cephalosome and 4 pedigerous somites; cephalosome and first pedigerous somite separate. Cephalosome slightly wider than long, bluntly rounded anteriorly, bulged laterally, indented in posterior third, with antennules and antennae visible in dorsal view. Cephalic ornamentation comprising anterior circular marking and a more posterior, less visible oval marking; an inverted T-structure of thickened chitin situated medially on dorsal side, between the circular and oval marking. First 4 pedigerous somites well developed, decreasing in length and width posteriorly. Urosome comprising short fifth pedigerous somite, narrowed genital segment in posterior third (Fig. 10F) and 2 free abdominal somites decreasing in width posteriorly. Second abdominal somite incised medially, about as long as preceding somite. Caudal rami subrectangular, slightly longer than wide; each ramus armed with 3 terminal setae – the innermost longest and thickest. Two long egg sacs (Fig. 10G), much longer than wide, reaches past longest furcal seta; each composed of 2 rows of brick-shaped eggs.

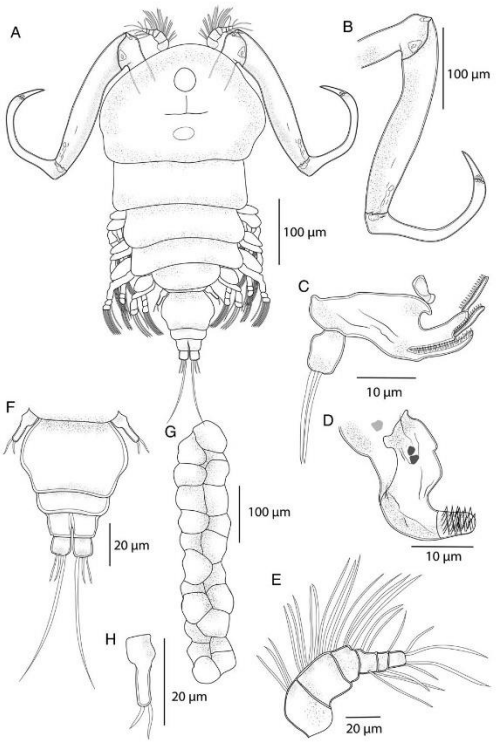


Fig. 10. *Ergasilus parvus* n. sp., adult female from *Spathodus erythrodon*. (A) Habitus, dorsal; (B) antenna, ventral; (C) mandible and maxilulle, ventral; (D) maxilla, ventral; (E) antennule, ventral; (F) abdomen and caudal rami; (G) egg sac, dorsal; (H) leg V, ventral.

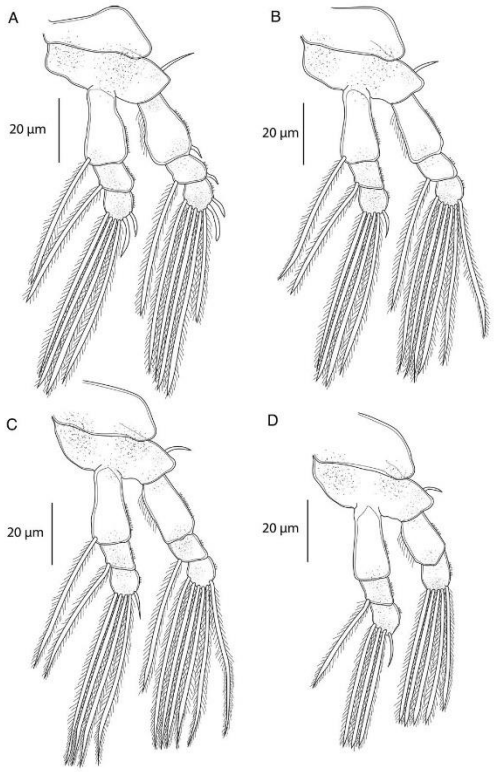


Fig. 11. *Ergasilus parvus* n. sp., adult female from *Spathodus erythrodon*. (A) Leg I, ventral; (B) leg II, ventral; (C) leg III, ventral; (D) leg IV, ventral.

Antennule (Fig. 10E) 6-segmented, tapering distally, armed with simple setae; setal formula from proximal to distal segments: 3–8–4–4–2–4.

Antenna (Fig. 10B) prehensile, composed of short coxobasis, 3-segmented endopod and strongly curved terminal claw. First endopodal segment markedly more robust than the second one; second endopodal segment and terminal claw evenly curved ventrally; third endopodal segment inconspicuous. Terminal claw about 1/5 length of second endopodal segment. Antenna without setules, spines or indentations.

Mouthparts (Fig. 10C and D) comprising mandible, maxillule and maxilla; maxilliped absent. Mandible consisting of 3 blades (anterior, middle and posterior); each blade with sharp teeth on anterior margin. Maxilulle a single lobe, bearing 2 equally long setae. Maxilla 2-segmented, comprising unarmed syncoxa and basis; basis distally with numerous sharp teeth on anterior margin.

Swimming legs I–IV; each comprising coxa, basis and 2 segmented rami (i.e. exopod, endopod) (Fig. 11). Rami of all legs 3-segmented, except 2-segmented exopod of leg IV. Segments distinct, typical of members of the genus. Interpodal plates of all legs lacking spinules. Armature on rami as follows (Roman and Arabic numerals indicating spines and setae, respectively) in Table 8.

Leg I (Fig. 11A) with unarmed coxa and basis with outer seta. Exopod 3-segmented; first segment with small outer spine; second segment with inner plumose seta and small outer spine; third segment with small spine on outer corner, long apical spine and 5 plumose setae. Endopod 3-segmented; first and second segment

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Table 8. Spine and setal formula of swimming legs of *E. parvus* n. sp.

	Coxa	Basis	Exopod	Endopod
Leg I	0–0	1–0	I–0; I–1; II–5	0–1; 0–1; II–4
Leg II	0–0	1–0	0–0; 0–1; 0–6	0–1; 0–1; I–4
Leg III	0–0	1–0	0–0; 0–1; 0–6	0–1; 0–1; I–4
Leg IV	0–0	1–0	0–0; 0–5	0–0; 0–1; I–3

each with plumose inner seta; third segment with small spine on outer corner, long apical spine and 4 plumose setae. Outer margins of both rami partly or completely covered with rows of spinules.

Legs II and III similar (Fig. 11B and C). Coxa unarmed, basis with outer seta. Exopod 3-segmented; first segment lacking armature; second segment with 1 plumose seta, lacking spine; third segment with 6 setae. Endopod 3-segmented; first and second segment each with 1 plumose seta; third segment with 4 plumose setae and 1 distal spine. Outer margins of both rami partly or completely covered with rows of spinules.

Leg IV (Fig. 11D) with unarmed coxa and basis having outer seta. Exopod 2-segmented; first segment longest with no armature; second segment with 5 plumose setae. Endopod 3-segmented; first segment lacking armature; second segment with 1 plumose seta; third segment with 3 plumose setae and distal spine. Outer margins of both rami partly or completely covered with rows of spinules.

Leg V (Fig. 10H) reduced but visible, bearing 2 simple seta located distally.

Specimens preserved in ethanol faint brown in colour; traces of a purple pigment in cephalosome sometimes observed after clearing in lactic acid.

Male: unknown.

Remarks

Based on the body shape and antenna morphology, *E. parvus* n. sp. is most similar to *E. latus* (Fryer, 1960), described from the mouthbrooding cichlid *Oreochromis niloticus* (Linnaeus, 1758) from Lake Turkana, Kenya (Fryer, 1960). Records of the latter species came also from Ghana (Thurston, 1970), the Niki River (Fryer, 1968), the River Galma (Shotter, 1977), Kitona (Fryer, 1963) and the Afram Basin, Mawli River and Peshi Lagoon (Paperna, 1969). *Ergasilus parvus* n. sp. is differentiated from *E. latus* by having: (i) a much smaller body size (475 *vs* 900); (ii) a small outer spine on the exopod of leg I; (iii) a seta on the second endopod segment of leg II; (iv) brick-shaped egg sacs (*vs* ovoid egg sacs in *E. latus*); (v) a less prominent leg V; and (vi) the presence of cephalic ornamentation (ovoid and circular marking) (*vs* only inverted T-structure present in *E. latus*).

Molecular characterization and phylogenetic position of Ergasilus *species from Lake Tanganyika within the Ergasilidae*

No intraspecific variability was detected for partial 18S and 28S rDNA sequences of *Ergasilus* species parasitizing cichlid fishes from Lake Tanganyika. The overall *p*-distance among *Ergasilus* species found for 18S and 28S rDNA sequences was 0.1 and 2% (see Table 9), respectively. Moreover, the 18S sequences displayed no or low (1 bp) interspecific variability; no differences were found among 18S rDNA sequences of *E. macrodactylus*, *E. parvus* n. sp. or *E. caparti* n. sp., or between sequences of *E. megacheir* or *E. parasarsi* n. sp. *Ergasilus parasarsi* n. sp. was revealed as the most genetically distant species to *E. caparti* n. sp. or *E. megacheir* (2.72%). The lowest values of interspecific differences (0.85%) were found between *E. macrodactylus* and *E. parvus* n. sp. or *E. megacheir*.

ML and BI analyses based on concatenated alignment including partial 18S and 28S rDNA sequences of Ergasilidae yielded trees with congruent topologies with similar nodal support values and revealed 4 well-supported groups (Fig. 12): (A) *Ergasilus* species from Lake Tanganyika cichlids, (B) *Sinergasilus* species and the *E. anchoratus* group, (C) Asian *Ergasilus* species and the *Neoergasilus japonicus* group and (D) *Paraergasilus* species and the *E. wilsoni* group. The present results are consistent with previously reported ergasilid phylogenies (Song *et al.*, 2008; Santacruz *et al.*, 2020; Kvach *et al.*, 2021) and suggest the polyphyletic status of the genus *Ergasilus*. Although *Ergasilus* species from Lake Tanganyika cichlids formed a well-supported clade, their position within Ergasilidae was not fully resolved due to the observed low support values as well as an insufficient amount of molecular data.

Key for identification of Ergasilus *species from Lake Tanganyika*

1. (2) Five-segmented antennule 3
2. (1) Six-segmented antennule 5
3. (4) Second endopodal segment of antenna with outer denticle near its distal end; leg V 2-segmented, with 1 seta on reduced proximal segment and 2 setae on distal segment; caudal ramus with 1 long and 3 short setae. ..... *E. flaccidus*
4. (3) Second endopodal segment of antenna with inner denticle near its proximal end; leg V reduced to 1 segment, with 4 setae; caudal ramus with 2 long and 2–3 short setae ..... *E. kandti*
5. (6) Each caudal ramus with 3 setae 7
6. (5) Each caudal ramus with 4 setae 9
7. (8) Second endopodal segment of antenna of similar diameter as first endopodal segment, with slight outer depression near its proximal end; cephalosome with smooth lateral margins, inverted T-structure having anteriorly recurved lateral ends (resembling a smile); gap between cephalosome and first thoracic segment clearly marked; leg V with 3 setae; 3-segmented abdomen ..... *E. sarsi*
8. (7) Second endopodal segment of antenna much thinner than first endopodal segment, without depression; cephalosome bulged laterally, with inverted T-structure lacking anteriorly recurved lateral ends; leg V with 2 setae; 2-segmented abdomen ..... *E. parvus*
9. (10) Second endopodal segment of antenna without depression; cephalosome trapezoidal, with inverted T-structure between circular and ovoid marking; leg V cylindrical, with 2 setae; 3-segmented abdomen; caudal ramus with 1 long and 3 short setae ..... *E. macrodactylus*
10. (9) Second endopodal segment of antenna with outer proximal depression 11
11. (12) Terminal claw of antenna with small inner denticle; second endopodal segment of antenna short and twisted; anterior edge of first endopodal segment of antenna with thin hyaline border; cephalosome quadrangular, with inverted T-structure between circular and ovoid marking; leg V extremely small, with 1 seta; 2-segmented abdomen ..... *E. megacheir*

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Table 9. Nucleotide comparison of the partial 28S rDNA sequences of family Ergasilidae based on 589 bp-long alignment

			1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
Acusicola	1.	*A. margulisae*		50	53	54	58	55	56	42	35	43	38	44	37	44	36	58	53	32	35	36	68	57	59
	2.	***E. caparti n. sp.***	8.57		13	11	16	13	61	49	44	56	41	55	50	50	49	60	54	50	51	52	73	63	64
	3.	***E. macrodactylus***	9.03	1.70		5	12	5	62	47	47	55	43	54	53	51	50	59	55	50	52	54	70	62	65
	4.	***E. megacheir***	9.20	1.87	0.85		16	8	63	51	51	59	44	58	55	53	51	61	58	52	54	56	71	63	66
	5.	***E. parasarsi n. sp.***	9.88	2.72	2.04	2.72		11	69	54	50	56	50	57	59	56	57	58	52	57	59	59	77	69	70
	6.	***E. parvus n. sp.***	9.37	2.21	0.85	1.36	1.87		66	51	51	55	48	56	57	55	53	61	57	55	57	59	74	66	69
	7.	*E. anchoratus*	9.54	10.37	10.54	10.71	11.73	11.22		61	50	66	52	63	56	63	47	75	69	55	58	55	20	10	11
	8.	*E. branini*	7.16	8.33	7.99	8.67	9.18	8.67	10.37		25	16	33	17	30	18	29	55	40	34	35	41	71	61	64
Ergasilus	9.	*E. hypomesi*	5.95	7.48	7.99	8.67	8.50	8.67	8.50	4.25		27	32	26	28	27	29	49	33	35	32	36	61	51	53
	10.	*E. parasilus*	7.33	9.52	9.35	10.03	9.52	9.35	11.22	2.72	4.59		37	5	35	22	36	54	35	45	44	48	79	66	69
	11.	*E. peregrinus*	6.64	6.97	7.31	7.48	8.50	7.82	8.84	5.61	5.44	6.29		36	35	39	33	48	50	32	35	32	63	52	57
	12.	*E. scalaris*	7.50	9.35	9.18	8.66	9.69	9.52	10.71	2.89	4.42	0.85	6.12		32	23	35	51	34	42	41	45	73	63	66
	13.	*E. sieboldi*	6.30	8.50	9.01	9.35	10.03	9.69	9.52	5.10	4.76	5.95	5.95	5.44		32	33	50	41	33	32	35	69	58	63
	14.	*E. turnidus*	7.50	8.50	8.67	9.01	9.52	9.35	10.71	2.72	4.93	3.74	6.63	3.91	5.44		33	52	37	46	37	45	73	63	64
	15.	*E. wilsoni*	5.11	8.33	8.50	8.67	9.86	9.01	7.99	4.93	4.93	5.46	5.61	5.95	5.61	5.61		51	44	20	23	27	59	48	50
	16.	*E. yaluzangbus*	9.88	10.20	10.03	10.37	9.86	10.37	12.76	9.35	8.33	9.18	8.16	8.67	8.50	8.84	8.67		57	51	55	54	85	75	77
Neoergasilus	17.	*N. japonicus*	9.03	9.18	9.35	8.86	8.84	9.69	11.73	6.80	6.61	5.95	8.50	5.78	6.97	6.29	7.48	9.69		45	48	44	78	68	68
	18.	*P. brevidigitus*	5.45	8.50	8.50	8.84	9.69	9.35	9.35	5.78	5.95	7.65	5.44	7.14	5.61	6.80	3.40	8.67	7.65		6	7	65	54	56
Paraergasilus	19.	*P. longidigitus*	5.95	8.67	8.84	9.18	10.03	9.69	9.52	5.95	5.44	7.48	5.95	6.97	5.44	6.29	3.40	9.35	7.82	1.87		13	66	55	57
	20.	*P. medius*	5.95	8.84	9.18	9.35	10.03	10.03	9.35	6.97	6.12	8.16	5.44	7.65	5.95	7.65	4.59	9.18	7.48	1.19	2.21		65	54	58
	21.	*S. major*	11.58	12.41	11.90	12.07	13.10	12.58	3.40	12.07	10.37	12.93	10.71	12.41	11.73	12.41	10.03	14.46	12.93	11.05	11.22	11.05		16	21
Sinergasilus	22.	*S. polycolpus*	9.71	10.71	10.54	10.71	11.73	11.22	1.70	10.37	8.67	11.22	8.84	10.71	9.86	10.71	8.16	12.76	11.58	9.18	9.35	9.18	2.72		11
	23.	*S. undulatus*	10.05	10.88	11.05	11.22	11.90	11.73	1.87	10.88	9.01	11.73	9.69	11.22	10.71	10.88	8.50	13.10	11.58	9.52	9.69	9.86	3.57	1.87	

P-distance (%) is given below the diagonal and the number of variable nucleotides above the diagonal. Conditional formatting highlights the lowest *p*-distances in dark grey while higher values in light grey.

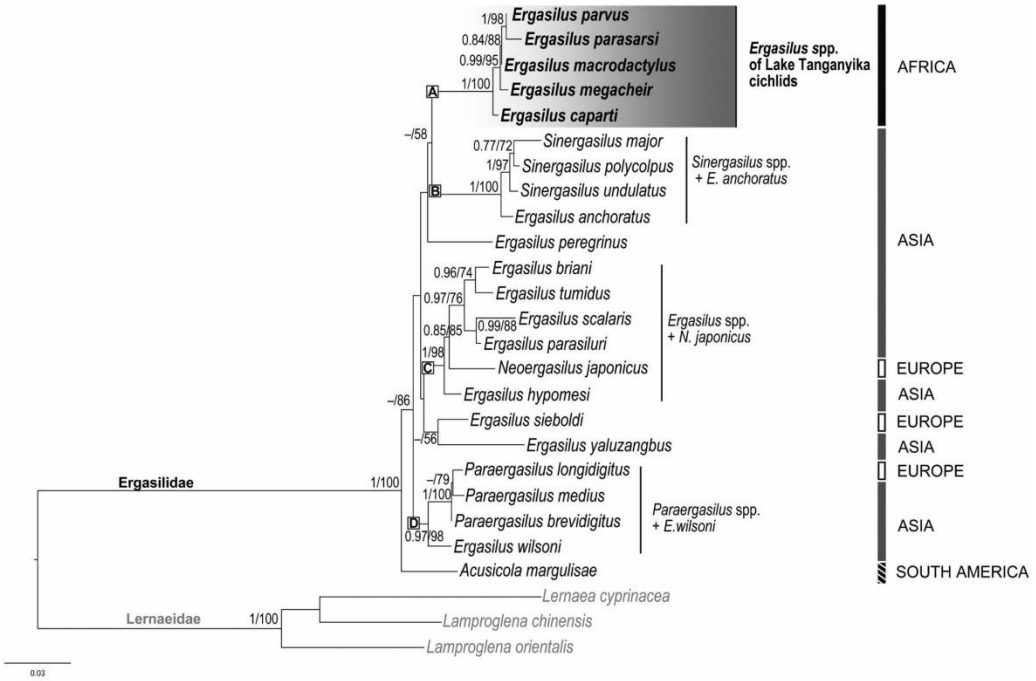


Fig. 12. Phylogenetic tree of Ergasilidae reconstructed by maximum likelihood. The tree is based on the combined sequences of partial genes coding 18S and 28S rRNA. Values along the branches indicate posterior probabilities from Bayesian inference and bootstrap values from maximum likelihood (dashes indicate values below 0.7 and 50, respectively). Letters (A)–(D) represent well-supported group of Ergasilidae.

12. (11) Terminal claw of antenna without a denticle 13
13. (14) Second endopodal segment of antenna with conspicuous depression formed by 2 ridges crossing each other; cephalosome hexagonal, posterior margin with medial indentation, with inverted T-structure between circular and ovoid marking; first pedigerous somite slightly tapering medially, with inverted U marking; leg V with 1 seta ..... *E. caparti*
14. (13) Second endopodal segment of antenna with indentation; cephalosome trapezoidal, with circular marking anterior to inverted T-structure; first pedigerous somite slightly tapering posteriorly; leg V with 2 setae ..... *E. parasarsi*

Discussion

Our investigation of crustacean parasites of cichlid fishes from Lake Tanganyika revealed the presence of 2 previously described and 3 new species of *Ergasilus* that were identified using a combined morphological and molecular approach. The occurrence of both previously described species (*E. macrodactylus* and *E. megacheir*) had already been confirmed in Lake Tanganyika in previous studies (Sars, 1909; Cunnington, 1920; Capart, 1944; Fryer, 1965); host species for *E. macrodactylus* were not recorded (Sars, 1909), and *E. megacheir* was found on 6 cichlids and 2 mochochid species of the genus *Synodontis* (Sars, 1909; Cunnington, 1920; Capart, 1944; Fryer, 1965). The present study brings new host records for these species: *E. marksmithi, G. permaxillaris, L. callipterus, P. microlepis* and *T. irsacae* for *E. macrodactylus* and *C. horei* and *S. diagramma* for *E. megacheir*. The occurrence of both these species has also been recorded in other areas of Africa; *E. megacheir* was collected from the gills of 1 cichlid species, *P. congicus* (Boulenger, 1897), in Lake Tumba in the Lower Congo (Fryer, 1964) and the presence of *E. macrodactylus* was confirmed in Lake Malawi on 4 cichlid species and 1 alestid (Fryer, 1956). However, the first description of *E. macrodactylus* as well as its occurrence in Lake Tanganyika (Sars, 1909) is doubtful, similarly to the description of *E. brevimanus* (Sars, 1909). The present results confirmed the presence of *E. macrodactylus* in Lake Tanganyika for the first time since Sars (1909), even though the overall size of the body is smaller than Fryer's redescription (Fryer, 1956) from Lake Malawi. The main difference between both descriptions is the segmentation of the antennule (Sars mentions 5-segmented antennule, Fryer 6-segmented antennule). From this point of view, the material from Lake Tanganyika matches the Fryer's description, since the antennule is clearly 6-segmented.

Until now, there were no studies on the genetic characteristics of African *Ergasilus* species; thus, the molecular data presented here represent the first insight into the phylogenetic relationships of this genus in Africa. In contrast to data on the well-documented distribution of ergasilid copepods among host species and regions, molecular data for this large taxon remain scarce over the whole range of its global distribution. Among the 30 valid Ergasilidae genera, molecular data are currently only available for 7 [*Acusicola* (Cressey, 1970); *Ergasilus*; *Gamispinus* (Thatcher and Boeger, 1984); *Miracetyma* (Malta, 1993); *Neoergasilus* (Yin,

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1956); *Paraergasilus* (Markevich, 1937); *Sinergasilus* (Yin, 1949) and *Therodamas* (Krøyer, 1863)]. Moreover, only molecular data belonging to species with an Asian origin were available for a long time (Song *et al.*, 2008). Recently, molecular data for the cosmopolitan species *E. sieboldi* (von Nordmann, 1832) collected from European perch in the Czech Republic, and *E. yandemontei* (Waicheim, Mendes Marques, Rauque and Viozzi, 2021) from atherinid silversides in Argentina and for a few other genera of Ergasilidae have been published (Ondračková *et al.*, 2019; Santacruz *et al.*, 2020; Kvach *et al.*, 2021; Waicheim *et al.*, 2021).

Based on the possibility to compare the genetic data of representatives of Ergasilidae, which are available in the GenBank database, molecular characterization of *Ergasilus* species in the present study was performed using 2 partial fragments of nuclear ribosomal DNA, i.e. 18S and 28S rDNA. Moreover, these 2 nuclear markers have been also applied in previous phylogenetic studies of Ergasilidae (Song *et al.*, 2008; Santacruz *et al.*, 2020; Kvach *et al.*, 2021). In the present study, no intraspecific genetic variability in both markers linked with host or locality was detected. However, low-intraspecific divergence in 18S and 28S rDNA was previously recorded in some representatives of ergasilid copepods (Song *et al.*, 2008; Ondračková *et al.*, 2019). The lake is 673 km-long, and only a relatively small part was sampled (the eastern shore of its northern end) and localities were roughly 100 km apart from each other. Therefore, a more extensive sampling comprising larger areas should be carried out to confirm genetic variability at the species level also in ergasilid species in Lake Tanganyika. Both genetic markers that were analysed differed in genetic distances (0.1% for 18S and 2% for 28S) among *Ergasilus* species in Lake Tanganyika. The 28S marker was shown to be much more efficient for species delimitation and the species found in this study were clearly resolved by means of its DNA sequence variability.

In contrast, the 18S marker was shown to be highly conservative within *Ergasilus* species found in Lake Tanganyika and almost no variability among species was observed. Previous phylogenetic studies confirmed that the 18S gene is more informative for resolving relationships between copepods at the genus and family levels (Huys *et al.*, 2006; Marrone *et al.*, 2013). Even though it is suitable for determining higher taxa, on the species level it does not show significant differences. This corresponds with previous studies which noted that 18S sequences are not suitable for determining the species-level richness of environmental samples, because they could underestimate species diversity (Tang *et al.*, 2012) and fail to resolve relationships between closely related species (Taniguchi *et al.*, 2004). Compared with the nuclear ribosomal genes, the commonly used barcoding gene, cytochrome c oxidase subunit I (COI mtDNA), has proven useful in free living copepods (Baek *et al.*, 2016; Mayor *et al.*, 2017). Moreover, COI data display high resolution at species level and may be also more efficient for revealing intraspecific variation (Tang *et al.*, 2012). Since there are only 7 COI sequences from *Ergasilus* species [*E. jaraquensis* (Thatcher and Robertson B.A., 1982) (2 sequences), *E. wilsoni* (1 sequence) and *Ergasilus* sp. (4 sequences) published in the GenBank on 17 October 2022], the analysis of COI marker is more than suitable in future studies regarding this group of copepodes. Nevertheless, the use of Folmer's (Folmer *et al.*, 1994) 'universal' COI primers has failed and showed to be problematic in the present study. Universal primers amplified non-ergasilid DNA pointing to contamination problems. Therefore, successful COI amplification in ergasilids will require above all the development of taxon-specific primers and to improve DNA barcoding protocols of parasitic copepods.

The phylogenetic reconstruction suggests that African ergasilids in Lake Tanganyika form a well-supported monophyletic lineage, though relationships within Ergasilidae still remain largely unresolved. This close relationship between Lake Tanganyika ergasilids may be related to the geographic origin of the species or to the endemism of their hosts. Assuming that parasite endemism correlates with the endemism of their hosts (Morand and Guégan, 2000) and assuming the existence of coevolution between parasites and their hosts, all newly described *Ergasilus* species could be considered as endemic to Lake Tanganyika. To date, at the level of parasitic crustaceans, 8 branchiuran species from the genus *Argulus* (Cunnington, 1913; Fryer, 1965, 1968; Rushton-Mellor, 1994*a*, 1994*b*), 2 species of *Lernaea* (Cunnington, 1914) and *Ergasilus flaccidus* (Fryer, 1965) collected from the endemic species *Oreochromis tanganicae* (Fryer, 1965) may also be considered as endemic species of Lake Tanganyika. The distributions of *E. megachier* and *E. macrodactylus* comprise other African areas (see below) and their host range includes also non-endemic host species. Molecular data would be particularly informative to support this hypothesis.

Overall, the relationships found within this family are consistent with previous phylogenetic analyses (Song *et al.*, 2008; Santacruz *et al.*, 2020; Kvach *et al.*, 2021; Oliveira *et al.*, 2021) and suggest that the genus *Ergasilus* is not monophyletic. Nevertheless, further morphological studies combined with molecular data are needed to elucidate the evolutionary relationships and origin of this diverse group of parasitic copepods.

Conclusion

The present study represents the first molecular and systematic update on ergasilids from Africa since more than 3 decades. The extent of the parasitic copepod fauna of the African region is most likely underestimated and harbours a great potential for discovering new species and new host records, using a similar approach combining morphological and molecular data. This study also highlights the need for further intensive genetic research on ergasilid species in order to elucidate the phylogenetic relationships within Ergasilidae. Future studies should consider using COI marker, since 18S rDNA is not suitable for species delimitation and 28S rDNA is limited.

Data availability. Type and voucher specimens were deposited in the Institute of Parasitology, Czech Academy of Sciences, České Budějovice, Czech Republic (accession codes Cr-33, Cr-34, Cr-35, Cr-36 and Cr-37). The sequences produced in this study were deposited in GenBank of NCBI at https://www.ncbi.nlm.nih.gov/ (accession codes OQ407465, OQ407466, OQ407467, OQ407468, OQ407469, OQ407470, OQ407471, OQ407472, OQ407473 and OQ407474).

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Author's contribution. R. M. and M. S. conceived and designed the study. E. Ř. collected parasitological material. R. M. performed morphological characterization and described the species. R. M. and M. S. performed molecular and phylogenetic analyses, and wrote the draft of the manuscript. E. Ř.

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reviewed descriptions of the species. All authors read and approved the final version of the manuscript.

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Conflict of interest. None.

Ethical standards. All applicable institutional, national and international guidelines for the care and use of animals were followed. This study was approved by the Animal Care and Use Committee of the Faculty of Science, Masaryk University in Brno (Czech Republic). This work is part of R. M.'s PhD study and it is a direct benefit to local fisheries biology as set within a broader ecosystem of current harvesting and an increasingly complex legislature.

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Paper 2

Míč, R., Řehulková, E., Šimková, A., Razanabolana, J. R., & Seifertová, M. (2024). New species of *Dermoergasilus* Ho & Do, 1982 (Copepoda: Cyclopoida: Ergasilidae) parasitizing endemic cichlid *Paretroplus polyactis* (Bleeker) in Madagascar. *Parasitology*, *151*(3), 319-336. https://doi.org/10.1017/S0031182024000088

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New species of *Dermoergasilus* Ho & Do, 1982 (Copepoda: Cyclopoida: Ergasilidae) parasitizing endemic cichlid *Paretroplus polyactis* (Bleeker) in Madagascar

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Abstract

Dermoergasilus madagascarensis n. sp. is described from the gills of *Paretroplus polyactis*, an endemic cichlid fish in Madagascar, using a combined morphological (light microscopy and SEM) and molecular approach (partial 18S rDNA, 28S rDNA, and COI sequences). The new species is characterized mainly by possessing: (i) roughly pentagonal cephalosome; (ii) antennal endopodal segments covered with slightly inflated membrane; (iii) maxillule bearing 2 equally long outer setae and a minute inner seta; (iv) interpodal sternites of swimming legs ornamented with 3–4 rows of spinules; (v) genital segment and first abdominal somite both barrel-shaped; and (vi) a caudal ramus projecting into a digitiform process with inconspicuous terminal seta and bearing 3 terminal setae. The obtained DNA sequences of Malagasy species represent the first molecular data for species of *Dermoergasilus*. The 28S rDNA phylogeny showed the affiliation of *D. madagascarensis* n. sp. to Ergasilidae and its sister relationship with cosmopolitan *Ergasilus sieboldi* von Nordmann, 1832. The first checklist for all species of *Dermoergasilus* is provided.

Introduction

Dermoergasilus Ho and Do, 1982 currently includes 12 valid species parasitizing freshwater, marine and brackish water fishes in Indian, Indo-West Pacific, Palaearctic and Afrotropic regions (Dogiel and Akhmerov, 1952; Cressey and Collette, 1970; Ho and Do, 1982; Byrnes, 1986; Oldewage and Van As, 1988; Ho *et al*., 1992; Kabata, 1992; El-Rashidy and Boxshall, 1999; El-Rashidy and Boxshall, 2001; Hassan *et al*., 2009; Ali and Adday, 2019). The host spectrum of *Dermoergasilus* species is broad and comprises various fishes belonging to 14 families, including mostly Mugilidae (12 species), Belonidae (4 species) and Sparidae (3 species). The number of host species parasitized by a *Dermoergasilus* species ranges from 1 (*Dermoergasilus cichlidus* Ali and Adday, 2019, *Dermoergasilus curtus* El-Rashidy and Boxshall, 2001 and *Dermoergasilus semicoleus* Cressey and Collette, 1970) to 8 [*Dermoergasilus amplectens* (Dogiel and Akhmerov, 1952)] (Table 1).

Dermoergasilus was proposed by Ho and Do (1982) to include 3 previously described species of *Ergasilus* (i.e. *Ergasilus amplectens* Dogiel and Akhmerov, 1952; *Ergasilus coleus* Cressey and Collette, 1970; *Ergasilus semicoleus* Cressey and Collette, 1970) possessing a combination of the following characters: (i) antenna, except terminal claw, covered with inflated transparent membrane; (ii) paired caudal rami each with a digitiform process; and (iii) middle segment of endopod of legs II and III possessing a single seta. Later, Byrnes (1986) described *Dermoergasilus acanthopagri* Byrnes, 1986 from sea breams (Sparidae) in Australia. Nevertheless, Gussev (1987) questioned the validity of the genus when he found several *Ergasilus* species possessing the antennal transparent membrane. Meanwhile, Oldewage and Van As (1988) described *Dermoergasilus mugilis* Oldewage and Van As, 1988 from grey mullet (Mugilidae) in Africa. Kabata (1992) confirmed the validity of the genus and stated that even just the digitiform process on paired caudal rami distinguishes *Dermoergasilus* from *Ergasilus*. The importance of the transparent membrane on antenna is also questioned since it is not well developed at some species of *Dermoergasilus*, and on the contrary, there are some species of *Ergasilus* which have transparent inflated membrane around the antenna (e.g. *E. acusicestraeus* El-Rashidy and Boxshall, 1999). Kabata (1992) described *Ergasilus intermedius* Kabata, 1992 and stated that this species is an intermediate form between *Ergasilus* and *Dermoergasilus*, later El-Rashidy and Boxshall (1999) transferred this species to *Dermoergasilus*. *Dermoergasilus varicoleus* Ho *et al*. (1992) parasitizing *Planiliza tade* (Fabricius) was described in India (Ho *et al*., 1992), whereas El-Rashidy and Boxshall (2001) described 3 species of *Dermoergasilus* from 6 species of grey mullet hosts (see Table 1): *D. longiabdominalis* El-Rashidy and Boxshall, 2001; *D. semiamplectens* El-Rashidy and Boxshall, 2001; and *D. curtus* El-Rashidy and Boxshall, 2001. *Dermoergasilus occidentalis* Hassan *et al*., 2009 was

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Table 1. Checklist of *Dermoergasilus* including host species, locality and site of collection

Dermoergasilus species	Host species	Host family	Locality	Site	References
D. acanthopagri Byrnes, 1986	*Acanthopagrus australis*	Sparidae	Gladstone, Australia	Gills	Byrnes (1986)
	Acanthopagrus berda	Sparidae	Daintree, Australia	Gills	Byrnes (1986)
	Acanthopagrus butcheri	Sparidae	Perth, Eden, Australia	Gills	Byrnes (1986)
D. amplectens (Dogiel and Akhmerov, 1952)	*Chanos chanos*	Chanidae	Poonthura, Trivandrum, India	Gills	Ho *et al.* (1992)
	Valamugil seheli (=*Crenimugil seheli*)	Mugilidae	Veli Lake, Trivandrum, India	Gills	Ho *et al.* (1992)
	Gerres setifer	Gerreidae	Neendakara, India	Gills	Ho *et al.* (1992)
	Liza argentea (=*Gracilimugil argenteus*)	Mugilidae	Serpentine Creek, Brisbane, Australia	Unknown	Kabata (1992)
	Hyporhamphus xanthopterus	Hemiramphidae	Poonthura, Trivandrum, India	Gills	Ho *et al.* (1992)
	Megalops cyprinoides	Megalopidae	Killiyar River, Trivandrum, India	Gills	Ho *et al.* (1992)
	Mugil cephalus	Mugilidae	Tumen-Ula River, Russia	Unknown	Dogiel and Akhmerov (1952)
			Kojima Bay, Okayama Prefecture, Japan	Gills	Ho and Do (1982)
			Tallebudgera Creek, South Queensland, Australia	Unknown	Kabata (1992)
			Mackay Fish Board, Australia	Unknown	Kabata (1992)
			Wakanoura, Japan	Gills	El-Rashidy and Boxshall (2001)
			Tsushima, Japan	Gills	El-Rashidy and Boxshall (2001)
			Kowie River, South Africa	Gills	El-Rashidy and Boxshall (2001)
	Etroplus maculatus (=*Pseudetroplus maculatus*)	Cichlidae	Veli Lake, Trivandrum, India	Gills	Ho *et al.* (1992)
D. cichlidus Ali and Adday, 2019	*Coptodon zillii*	Cichlidae	Shatt Al-Arab River, Al-Hartha District, Iraq	Gills	Ali and Adday (2019)
			Pond of Marine Sciences Centre, Basrah, Iraq	Gills	Ali and Adday (2019)
D. coleus (Cressey in Cressey and Collette, 1970)	*Strongylura urvillii*	Belonidae	Philippines	Gills	Cressey and Collette (1970)
	Strongylura strongylura	Belonidae	Cagayan de Misamis, Mindanao, Philippines	Gills	Cressey and Collette (1970)
			Sandakan Bay, Borneo, Malaysia	Gills	Cressey and Collette (1970)
			Porto Novo, Madras, India	Gills	Cressey and Collette (1970)
	Xenentodon cancila	Belonidae	Travancore, India	Gills	Cressey and Collette (1970)
			Calcutta, India	Gills	Cressey and Collette (1970)
D. curtus El-Rashidy and Boxshall, 2001	*Rhinomugil squamipinnis* (=*Rhinomugil corsula*)	Mugilidae	Alahabad, India	Gills	El-Rashidy and Boxshall (2001)
D. intermedius (Kabata, 1992)	*Maccullochella macquariensis*	Percichthyidae	Moreton Bay, Queensland, Australia	Unknown	Kabata (1992)
	Tandanus tandanus	Plotosidae	Macintyre River, Queensland, Australia	Unknown	Kabata (1992)
			Taroon, Queensland, Australia	Unknown	Kabata (1992)
	Fluvialosa richardsoni (=*Nematalosa erebi*)	Dorosomatidae	Macintyre River, Queensland, Australia	Unknown	Kabata (1992)
	Plectroplites ambiguus (=*Macquaria ambigua*)	Percichthyidae	Macintyre River, Queensland, Australia	Unknown	Kabata (1992)

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D. longiabdominalis El-Rashidy and Boxshall, 2001	*Valamugil engeli* (=*Osteomugil engeli*)	Mugilidae	Calabato, Mindanao, Philippines	Gills	El-Rashidy and Boxshall (2001)
	Valamugil cunnesius (=*Osteomugil cunnesius*)	Mugilidae	Tamatave, Madagascar	Gills	El-Rashidy and Boxshall (2001)
			Mindanao, Philippines	Gills	El-Rashidy and Boxshall (2001)
			Mangalore, India	Gills	El-Rashidy and Boxshall (2001)
***D. madagascarensis* n. sp.**	***Paretroplus polyactis***	**Cichlidae**	**Canal des Pangalanes (at Andevoranto), Madagascar**	**Gills**	**Present study**
D. mugilis Oldewage and Van As 1988	*Mugil cephalus*	Mugilidae	Mouth of Keurbooms River, Cape Province, South Africa	Gills	Oldewage and Van As (1988)
			Bushman's River mouth, South Africa	Gills	Oldewage and Van As (1988)
D. occidentalis Hassan *et al.*, 2009	*Tandanus bostocki*	Plotosidae	Jalbarragup, Blackwood River, Western Australia	Gills	Hassan *et al.* (2009)
	Galaxias occidentalis	Galaxiidae	Swan River, Western Australia	Gills	Hassan *et al.* (2009)
D. semiamplectens El-Rashidy and Boxshall, 2001	*Sicamugil hamiltoni*	Mugilidae	Sittang River, Myanmar	Gills	El-Rashidy and Boxshall (2001)
	Valamugil cunnesius (=*Osteomugil cunnesius*)	Mugilidae	China	Gills	El-Rashidy and Boxshall (2001)
	Liza subviridis (=*Planiliza subviridis*)	Mugilidae	Calcutta, India	Gills	El-Rashidy and Boxshall (2001)
	Liza parsia (=*Planiliza parsia*)	Mugilidae	Calcutta, India	Gills	El-Rashidy and Boxshall (2001)
D. semicoleus (Cressey in Cressey and Collette, 1970)	*Strongylura krefftii*	Belonidae	Oenpalli, Alligator River, Australia	Gills	Cressey and Collette (1970)
D. varicoleus Ho *et al.*, 1996	*Liza abu* (=*Planiliza ab*)	Mugilidae	Shatt Al-Arab River, Iraq		Khamees and Mhaisen (1995) and Ho *et al.* (1996)
	Liza subviridis (=*Planiliza subviridis*)	Mugilidae	Calcutta, India	Gills	El-Rashidy and Boxshall (2001)
			Orissa, India	Gills	El-Rashidy and Boxshall (2001)
			Madras, India	Gills	El-Rashidy and Boxshall (2001)
			Bombay, India	Gills	El-Rashidy and Boxshall (2001)
	Planiliza tade	Mugilidae	Veli Lake, Trivandrum, India	Gills	Ho *et al.* (1992)
	N/A	Cyprinidae		Unknown	Ali and Adday (2019)
	N/A	Siluridae		Unknown	Ali and Adday (2019)
Dermoergasilus sp.	*Cyprinus carpio*	Cyprinidae	Marine Sciences Centre ponds, Basrah, Iraq	Gills	Ahmed and Ali (2013)

N/A, data not available.
The valid names of fish hosts are given in parentheses.

described from eeltail catfishes (Plotosidae) and galaxiids (Galaxiidae) in Australia (Hassan *et al.*, 2009). Ahmed and Ali (2013) reported *Dermoergasilus* sp. from common carp (*Cyprinus carpio* L.) in Iraq but did not provide further morphological identification. Most recently, *Dermoergasilus cichlidus* Ali and Adday, 2019 was described from redbelly tilapia [*Coptodon zillii* (Gervais)] in Iraq (Ali and Adday, 2019).

Until now, there are only a few parasitic crustacean records from freshwater fishes in Madagascar. Fryer (1968) questioned whether it is due to the lack of scientific interest or because of their true absence. The only record of a parasitic copepod on this island is *Dermoergasilus longiabdominalis* El-Rashidy and Boxshall, 2001 from *Osteomugil engeli* (Bleeker) (El-Rashidy and Boxshall, 2001). From other parasitic crustaceans recorded in the region only the occurrence of parasitic isopod *Cymothoa borbonica* Schioedte & Meinert, 1884 from the mouth of the freshwater cichlid fish *Ptychochromis oligacanthus* (Bleeker) is reported by (Trilles, 1975).

The other parasitic crustaceans recorded from this area are associated with the marine fish species (e.g. Barnard, 1960; Cressey, 1963; Trilles, 1975, 1979, 2008; Benz, 2006); or mud shrimps (Humes *et al.*, 1958); sea stars (Humes and Cressey, 1958; Humes and Ho, 1966; Humes, 1971); gorgonaceans (Humes, 1974); holothurians (Humes and Cressey, 1959, 1961; Humes, 1967); corals (Humes, 1962; Humes and Frost, 1964; Humes and Ho, 1967); molluscs (Humes and Ho, 1965); antipatharians (Humes, 1967).

During the investigation of gill parasites of cichlid fishes in Madagascar, *Dermoergasilus* specimens were collected from the gills of *Paretroplus polyactis*. Description of new *Dermoergasilus* species was performed using morphological study (light and SEM microscopy), and a molecular study using ribosomal and mitochondrial DNA sequences (partial 18S rDNA, 28S rDNA and COI sequences). In addition, to investigate the relationship of *D. madagascarensis* n. sp. to other representatives of Ergasilidae, phylogenetic analyses were performed.

Materials and methods

Fish collection

During a parasitological survey in April 2016, 100 fish specimens were examined for the presence of metazoan parasites (see Supplementary Table 1) Examined fish included mainly representatives of the family Cichlidae (92 specimens), some non-cichlid fishes living in sympatry with cichlids were also examined [4 specimens of Gobiidae (*Glossogobius giuris* (Hamilton) and *Glossogobius* sp.)], 2 specimens of Mugilidae [*Osteomugil robustus* (Günther) and *Planiliza macrolepis* (Smith) and Aplocheilidae (*Pachypanchax omalonotus* (Duméreil))]. Fishes were sampled in 4 localities (Fig. 1): (1) Lake Ravelobe (Ankarafantsika National Park) 16°18′23.14″S–46°48′43.32″E, (2) the Anjingo River (near Antsohihy) 14°50′40.89″S–48°14′43.36″E, (3) the crater lakes of Mont Passot (on Nosy Be Island) 13°19′1.84″S–48°14′3.60″E, and (4) the Canal des Pangalanes (at Andevoranto) 18°57′17.50″S–49°6′29.90″E. These areas belong to the eastern basins and freshwater systems of north-western Madagascar, all recognized as hotspots of Malagasy fish diversity (Benstead *et al.*, 2003). All fish specimens were transported alive to the field laboratory, sacrificed by severing the spinal cord, and dissected within 48 h following classical parasitological dissection procedure (Ergens and Lom, 1970). Fish specimens were measured and identified by local co-workers familiar with the fish fauna, and the identification was subsequently confirmed using sequences of the cytochrome mitochondrial gene (see Šimková *et al.*, 2019 for detailed information). The present study was part of a larger investigation concerning transmission of parasites from introduced cichlids to native Malagasy fish (Šimková *et al.*, 2019).

Parasite collection and identification

Live copepods were collected from the gills using fine needles and processed for morphological and molecular purposes, as described in Míč *et al.* (2023). The mounted specimens in GAP (mixture of glycerine and ammonium picrate) or pure glycerine were studied using an Olympus BX61 microscope equipped with phase contrast optics. Drawings of the copepods were made using an Olympus drawing attachment and edited with a graphic tablet (Wacom Intuos5 Touch) compatible with Adobe Illustrator and Adobe Photoshop (Adobe Systems Inc., San Jose, CA, USA). All measurements (in micrometers) were taken using digital image analysis software (Olympus Stream Motion v. 1.9.3) and are presented as the range followed by the mean ($n = 10$).

For scanning electron microscope analysis, 5 specimens fixed in 70% ethanol were dehydrated in an increasing ethanol grades, dried in a CPD 030 critical point drying apparatus (Bal-tec, Balzers, Liechtenstein) using liquid CO_2, mounted on aluminium stubs with double sided adhesive discs, coated with gold in a SCD 040 sputter coating unit (OC Oerlikon Balzers Coating, Balzers, Liechtenstein) and examined in a VEGA scanning electron microscope operating at 20 kV.

For comparative purposes, specimens of the following 4 previously described species of *Dermoergasilus* available in the Natural History Museum (London, UK; BMNH) were examined: *D. amplectens* (BMNH 1999.1399-1401), *D. longiabdominalis* (BMNH 1999.1321), *D. semiamplectens* (BMNH 1999.1341-1374; BMNH 1999.1376-1377) and *D. varicoleus* (BMNH 1999.1412-1417).

The type specimens of the copepods collected in the present study were deposited in the Institute of Parasitology, Czech Academy of Sciences, České Budějovice, Czech Republic. Prevalence (percentage of infected fish) and mean intensity of infection (mean number of parasites per infected host) were calculated following Bush *et al.* (1997).

Molecular and phylogenetic analyses

Genomic DNA was isolated separately from each parasite specimen (or a part of its body) using DNeasy®Blood & Tissue Kit (Qiagen, Hilden, Germany) according to the manufacturer's instructions. For molecular characterization, partial sequences of 1 mitochondrial gene (COI) and 2 nuclear ribosomal regions (18S and 28S rDNA) were amplified by using the primer sets listed in Table 2. PCRs for 18S and 28S rDNA were carried out in a total volume of 20 μL containing 3 μL of DNA extract, 1× PCR buffer (Fermentas), 2.5 mM $MgCl_2$, 0.2 mM of each dNTP, 0.2 μM of each primer, 0.1 BSA and 1 U of Taq polymerase (Fermentas). Amplification was performed under the following conditions: 94°C for 5 min; 39 cycles of 94°C for 30 s; an annealing temperature of 52°C for 30 s; and 72°C for 1 min, with a final extension step at 72°C for 5 min. PCR for COI was carried out in a total volume of 50 μL containing 1 μL of DNA extract, 1× PCR buffer (Fermentas), 2.5 mM $MgCl_2$, 0.5 mM of each dNTP, 0.5 μM of each primer, 0.1 BSA and 2 U of Taq polymerase (Fermentas). Amplification was performed under the following conditions: 95°C for 5 min; 40 cycles of 95°C for 1 min; an annealing temperature of 45°C for 1 min; and 72°C for 30 s, with a final extension step at 72°C for 7 min. The PCR amplicons were checked by electrophoresis on 1.5% agarose gels stained with Good View™ (Amplia s.r.o., Bratislava, Slovakia), and PCR products of the required length were purified using ExoSAP-IT™ (Affymetrix

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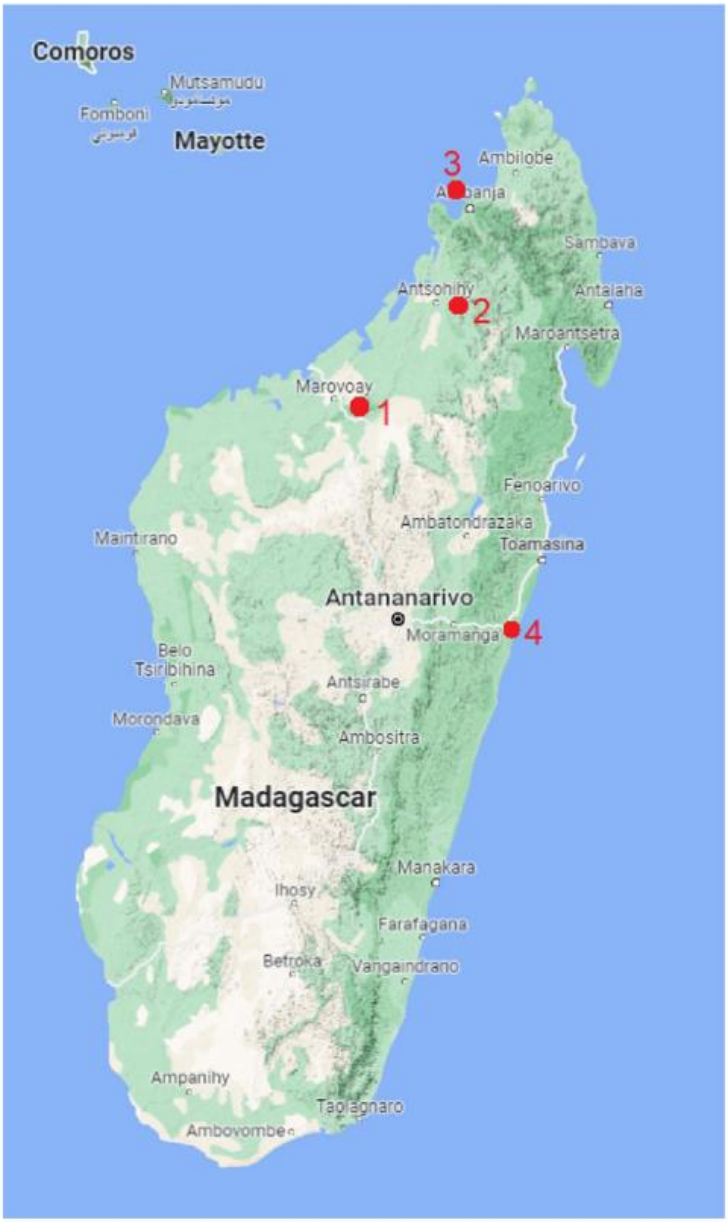


Figure 1. Map of Madagascar indicating the sampling localities: (1) Lake Ravelobe; (2) Anjingo River; (3) crater lakes of Mont Passot; (4) Canal des Pangalanes.

Inc., Santa Clara, USA), following the manufacturer's instructions. Purified products were directly sequenced using the same primers as those for PCR. DNA sequencing was carried out using BigDye® Terminator v3.1 Cycle Sequencing Kit (Applied Biosystems by Thermo Fisher Scientific, Prague, Czech Republic) and a 3130 Genetic Analyzer (Applied Biosystems). The obtained sequences were assembled and edited using Sequencher software (Gene Codes Corp., Ann Arbor, MI, USA). Newly generated sequences of 18S rDNA, 28S rDNA and COI were deposited in GenBank under accession numbers PP115569 (28S rDNA), PP115568 (18S rDNA) and PP117929-PP117934 (COI). Molecular vouchers (hologenophores, paragenophores; Pleijel *et al.*, 2008) were deposited in the Institute of Parasitology, Czech Academy of Sciences, České Budějovice, Czech Republic.

To investigate the phylogenetic position of *Dermoergasilus madagascarensis* n. sp., to the representatives of parasitic Cyclopoida, the sequences of 28S rDNA of the species belonging to 9 genera were retrieved from GenBank and Bold databases

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Table 2. List of primers used for PCR amplifications of mitochondrial and nuclear markers in the present study

Locus	Primer name	Direction	Sequence (5´–3´)	Size of the fragment (bp)	Ta (°C)	References
18S	18SF	Forward	AAG GTG TGM CCT ATC AAC T	1383	52°C	Song *et al.* (2008)
	18SR	Reverse	TTA CTT CCT CTA AAC GCT C			
28S	28SF	Forward	ACA ACT GTG ATG CCC TTA G	668	52°C	Song *et al.* (2008)
	28SR	Reverse	TGG TCC GTG TTT CAA GAC G			
CO1	LCO1490	Forward	GGT CAA CAA ATC ATA AAG ATA TTG G	675	45°C	Folmer *et al.* (1994)
	ErgHCO	Reverse	TAR ACY TCM GGR TGA CCR AAA AAY CA			Present study

Ta, annealing temperature.

(for details, see Table 3). Three species of the family Lernaeidae, *Lernaea cyprinacea* (Linnaeus, 1758), *Lamproglena chinensis* Yü, 1937 and *Lamproglena orientalis* Markevich, 1936 were used as outgroup. Sequences were aligned using MAFFT v.7 (Katoh and Standley, 2013). Gaps and ambiguously aligned regions were removed from the alignments with Gblocks v0.91b (Talavera and Castresana, 2007) using settings for a less stringent selection. ModelFinder (Kalyaanamoorthy *et al.*, 2017) was employed to select the most appropriate model of DNA evolution. The most suitable evolutionary model for the partial sequence of 28S rDNA was TIM3 + F + I. The phylogenetic reconstruction was performed using maximum likelihood (ML) and Bayesian inference (BI) methods. ML analyses were run using IQ-TREE (Nguyen *et al.*, 2015) on the W-IQ-TREE webserver (Trifinopoulos *et al.*, 2016) and nodal support for the tree was assessed through ultrafast bootstrap approximation with 1000 replicates (Hoang *et al.*, 2018). BI analysis was carried out in MrBayes 3.2.6 (Huelsenbeck and Ronquist, 2001) using the CIPRES platform (Miller *et al.*, 2010), the analysis included 2 simultaneous runs of Markov chain Monte Carlo for 10^6 generations, sampling every 100 generations, with a 'burn-in' of 25%. The results were checked in Tracer v. 1.7.1 (Rambaut *et al.*, 2018) to assess chain convergence. The trees were visualized and edited in FigTree v. 1.4.3 (Rambaut, 2012). Genetic distances (uncorrected p-distance) were calculated in MEGA v. 11 (Tamura *et al.*, 2021).

Results

Endemic cichlid *P. polyactis* from the Canal des Pangalanes (locality 4 in Fig. 1) was the only host species (out of 15 species examined) infected by parasitic copepods and exhibited intensity of infection ranging from 5 to 283 (mean 59) per individual fish. Overall, 20 specimens of *P. polyactis* were examined and the prevalence of *Dermoergasilus* parasites was 90%. Total prevalence of *Dermoergasilus* among all examined fishes in the study was 18%.

The copepod specimens collected from *P. polyactis* were identified as *Dermoergasilus* based on the diagnostic morphological characters according to Ho and Do (1982), specifically: (i) antenna, except terminal claw, covered with inflated transparent membrane; (ii) paired caudal rami each with a digitiform process; and (iii) middle segment of endopod of legs II and III possessing a single seta.

Family Ergasilidae Burmeister, 1835
Genus *Dermoergasilus* Ho & Do, 1982

Dermoergasilus madagascarensis n. sp.
Type-host: *Paretroplus polyactis* (Bleeker, 1878) (Cichlidae, Cichliformes)

Type-locality: Canal des Pangalanes (at Andevoranto) (18°57′17.50″S, 49° 6′29.90″E), Madagascar

Type and voucher material: Holotype (adult female): Cr-39 (1 specimen). Paratypes (adult females): Cr-39 (3 specimens). Hologenophores (adult females): Cr-39 (16 specimens).

Site on host: Gill filaments.

Prevalence and intensity of infection: 90% (18 fish infected/20 fish examined); 5–283 (mean 59) copepods per infected host.

ZooBank registration: urn:lsid:zoobank.org:act:5A5C2DCB-CCAB-4545-B6F4-F416CC22B10D

Representative DNA sequences: A 1384 bp long 18S rDNA sequence, 674 bp long 28S rDNA sequence and 9 COI sequences of 678 bp long obtained from 10 specimens are deposited in the NCBI GenBank database under the accession numbers PP115569 (28S rDNA), PP115568 (18S rDNA) and PP117929-PP117934 (COI), respectively.

Etymology: The species was named after the type locality, Madagascar Island, from which it was first discovered.

Description

Adult female. [Based on 10 specimens; Figs 2–5; measurements in Table 4].

Prosome 5-segmented, composed of cephalothorax and 3 free pedigerous somites (PS-1 to PS-4) (Fig. 2A). Cephalosome roughly pentagonal, rounded and slightly tapering anteriorly; antennules and antennae visible in dorsal view (Fig. 5A and B). Cephalic ornamentation comprising inverted T-shaped marking, sensory setae and pits with bilaterally symmetrical distribution on dorsal side. Rostrum shieldlike with 6 sensillae and 3 integumental pores (Figs. 3D and 5C). PS-1 elongated, with bilateral indentations just posterior to midlength; dorsal surface with slight T-shaped and rectangular depression situated anterior and posterior, respectively, to the constricted part; dorsal ornamentation comprising circular indentations situated just posterior to cephalosome and pair of sensillae near posterior margin. PS-2 to PS-4 decreasing gradually in width posteriorly, the three together barrel-shaped. Dorsal surface of each segment possessing anteriorly arising trapezoidal plate, sensillae and pits with bilaterally symmetrical distribution.

Urosome comprising fifth pedigerous somite (PS-5), genital double somite, and 3 free abdominal somites (AS-1 to AS-3) (Fig. 3A). PS-5 reduced, smaller and thinner than prosome somites, unornamented. Genital segment large, barrel-shaped, with transverse row of spinules and pair of hook-shaped ornamentation on ventral side. Free abdominal somites decreasing in width posteriorly. AS-1 wider than long (1.2–1.3 times), almost 3 times larger than AS-2, bearing transverse row of spinules at widest part. AS-2 slightly larger than AS-3, with transverse row of spinules at midlength. AS-3 (anal somite) deeply incised posteromedially, with spinules on posterior margin.

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Table 3. List of parasitic copepods used for phylogenetic analyses and calculation of p-distances, including their host species, collection locality, and accession numbers for partial 18S, 28S rDNA and COI sequences from database GenBank and Bold (indicated with *)

				GenBank/Bold accession numbers			
Parasite species	Host species	Host family	Locality	18S	28S	COI	References
Ergasilidae							
Acusicola margulisae	*Amphilophus citrinellus*; *Oreochromis* sp.	Cichlidae	Nicaragua	MN852694	MN852851	MN85438–MN85470	Santacruz *et al.* (2020)
***Dermoergasilus madagascarensis* n. sp.**	***Paretroplus polyactis***	**Cichlidae**	**Canal des Pangalanes, Madagascar**	**PP115568**	**PP115569**	**PP117929–PP117934**	**Present study**
Ergasilus anchoratus	*Tachysurus fulvidraco*	Bagridae	Baoan Lake, China	DQ107564	DQ107528	–	Song *et al.* (2008)
Ergasilus auritus	*Gasterosteus aculeatus*	Gasterosteidae	Nova Scotia, Canada	–	–	ECTCR091*	–
Ergasilus briani	*Misgurnus anguillicaudatus*	Cobitidae	Dangjiangkou, China	DQ107572	DQ107532	–	Song *et al.* (2008)
Ergasilus caeruleus	*Lepomis gibbosus x macrochirus*; *L. gibbosus*; *L. macrochirus*; *Notropis* sp.; plankton	Centrarchidae, Cichlidae	Lake Opinicon, Canada; Ottawa River, Canada; Oneida Lake, USA	–	–	ECTCR003*, ECTCR005*, ECTCR006*, ECTCR007*, ECTCR008*, ZOOPS258*, ZOOPS259*, ZOOPS260*, ZOOPS351*, ZOOPS353*, ZOOPS432*, ZOOPS433*	
Ergasilus caparti	*Neolamprologus brichardi*	Cichlidae	Lake Tanganyika, Burundi	OQ407468	OQ407472	–	Mič *et al.* (2023)
Ergasilus centrarchidarum	*Ambloplites rupestris*; *Lepomis gibbosus*; *Micropterus salmoides*; plankton	Centrarchidae	Lake Opinicon, Canada; St. Lawrence River, Canada, Richelieu River, Canada; Oneida Lake, USA	–	–	ECTCR001*, ECTCR009*, ECTCR037*, ECTCR038* ECTCR052*, ECTCR053*, ECTCR054*, ECTCR055*, ZOOPS071*, ZOOPS072*, ZOOPS073*, ZOOPS074*, ZOOPS075*	–
Ergasilus chautauquaensis	Plankton	–	Lake Erie, USA	–	–	ZOOPS076*; ZOOPS077*; ZOOPS078*	–
Ergasilus hypomesi	*Acanthogobius hasta*	Gobiidae	Dangjiangkou, China	DQ107573	DQ107539	–	Song *et al.* (2008)
Ergasilus jaraquensis	–	–	–	–	–	MF651988, MF651989	Lima *et al.* (2017)
Ergasilus kandti	–	–	Kenya	–	–	–	Unpublished data
Ergasilus lamellifer	*Hydrocynus forskahlii*	Alestidae	Sudan	–	–	–	Unpublished data
Ergasilus lizae	*Fundulus diaphanus*	Fundulidae	Richelieu River, Canada	–	–	ECTCR024*, ECTCR025*, ECTCR026*, ECTCR039*	–
Ergasilus luciopercarum	*Perca flavescens*; plankton	Percidae	Lake Erie, Canada; Oneida Lake, USA	–	–	ECTCR078*, ECTCR079*, ECTCR080*, ZOOPS060*, ZOOPS061* ZOOPS062*, ZOOPS063*, ZOOPS064*, ZOOPS628*, ZOOPS629*, ZOOPS630*	–

(*Continued*)

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Table 3. (*Continued.*)

				GenBank/Bold accession numbers			
Parasite species	Host species	Host family	Locality	18S	28S	COI	References
Ergasilus macrodactylus	*Gnathochromis permaxillaris*	Cichlidae	Lake Tanganyika, Burundi	OQ407465	OQ407470	–	Mič *et al.* (2023)
Ergasilus megacheir	*Simochromis diagramma*	Cichlidae	Lake Tanganyika, Burundi	OQ407466	OQ407471	–	Mič *et al.* (2023)
Ergasilus megaceros	Plankton	–	Dickinson Lake, USA; Oneida Lake, USA	–	–	ZOOPS065*, ZOOPS066*, ZOOPS067*, ZOOPS068*, ZOOPS069*, ZOOPS070*, ZOOPS257*, ZOOPS437*, ZOOPS438* ZOOPS440*, ZOOPS439*, ZOOPS441*	–
Ergasilus nodosus	Bagrus bajad	Bagridae	Sudan	–	–	–	Unpublished data
Ergasilus parasarsi	*Simochromis diagramma*	Cichlidae	Lake Tanganyika, Burundi	OQ407467	OQ407473	–	Mič *et al.* (2023)
Ergasilus parasiluri	*Tachysurus fulvidraco*	Bagridae	Dangjiangkou, China	DQ107568	DQ107536	–	Song *et al.* (2008)
Ergasilus parvitergum	–	–	Kerala Coast, India	–	–	OP871074	Reshmi and Kappalli (2022)
Ergasilus parvus	*Spathodus erythrodon*	Cichlidae	Lake Tanganyika, Burundi	OQ407469	OQ407474	–	Mič *et al.* (2023)
Ergasilus peregrinus	*Siniperca chuatsi*	Sinipercidae	Dangjiangkou, China	DQ107577	DQ107531	–	Song *et al.* (2008)
Ergasilus scalaris	*Tachysurus dumerili*	Bagridae	Poyang Lake, China	DQ107565	DQ107538	–	Song *et al.* (2008)
Ergasilus sieboldi	*Perca fluviatilis*, *Sparus aurata*	Percidae, Spaidae	U Jezu, Czech Republic	MW810238	MW810242	–	Kvach *et al.* (2021)
Ergasilus sp. 1	*Clarias gariepinus*	Clariidae	Sudan	–	–	–	Unpublished data
Ergasilus sp. 2	–	–	Kenya	–	–	–	Unpublished data
Ergasilus tumidus	*Acheilognathus taenianalis*	Acheilognathidae	Niushan Lake, China	DQ107569	DQ107535	–	Song *et al.* (2008)
Ergasilus versicolor	–	–	Oneida Lake, USA	–	–	ZOOPS261*, ZOOPS262*, ZOOPS263*, ZOOPS264*, ZOOPS265*	–
Ergasilus wilsoni	–	–	South Korea	KR048765	KR048843	KR049036	Baek *et al.* (2016)
Ergasilus yaluzangbus	*Oxygymnocypris stewartii*	Cyprinidae	Lasa River, Tibet	DQ107578	DQ107540	–	Song *et al.* (2008)
Gamispinus diabolicus	–	–	–	MF651978	–	MF651982, MF651983	Lima *et al.* (2017)
Miracetyma sp.	–	–	–	MF651981	–	MF651984, MF651985, MF651986, MF651987	Lima *et al.* (2017)
Neoergasilus japonicus	*Lepomis gibbosus*, *Scardinius erythrophthalmus*	Centrarchidae, Cyprinidae	Rohlík, Czech Republic; U Jezu, Czech republic; Hvězda, Czech republic; Babice, Czech republic; South Korea	MH167970	MH167968	KR049037, MZ964932, MZ964933, MZ964934, MZ964935, MZ964936	Ondračková *et al.* (2019); Kvach *et al.* (2021) and Vasquez *et al.* (2022)
Paeonodes subviridis	–	–	Kerala Coast, India	–	–	OP425700	Reshmi and Kappalli (2022)

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Paraergasilus brevidigitus	*Cyprinus carpio*	Cyprinidae	Tangxun Lake, China	DQ107576	DQ107530	–	Song *et al.* (2008)
Paraergasilus longidigitus	*Abramis brama, Perca fluviatilis, Scardinius erythrophthalmus*	Leuciscinae, Percidae,	Pahrbek, U Jezu, Czech Republic	MW810239	MW810243	–	Kvach *et al.* (2021)
Paraergasilus medius	*Ctenopharyngodon idella*	Xenocyprididae	Tangxun Lake, China	DQ107574	DQ107529	–	Song *et al.* (2008)
Sinergasilus major	*Ctenopharyngodon idella*	Xenocyprididae	Tangxun Lake, China; Danube River	DQ107558	DQ107524	–	Song *et al.* (2008)
Sinergasilus polycolpus	*Hypophthalmichthys molitrix*	Xenocyprididae	Tangxun Lake, China; Jingzhou, China	DQ107563	DQ107525	KR263117	Song *et al.* (2008) and Feng *et al.* (2016)
Sinergasilus undulatus	*Cyprinus carpio*	Cyprinidae	Tangxun Lake, China	DQ107563	DQ107525	MW080644	Song *et al.* (2008) and Hua (2020)
Therodamas longicollum	*Leporinus fasciatus*	Anostomidae	Jarilandia, Brazil	MW652731	–	–	Oliveira *et al.* (2021)
Lernaeidae							
Lamproglena chinensis	*Channa argus*	Channidae	Dangjiangkou, China	DQ107553	DQ107545	–	Song *et al.* (2008)
Lamproglena orientalis	*Chanodichthys dabryi*	Xenocyprididae	Tangxun Lake, China	DQ107549	DQ107542	–	Song *et al.* (2008)
Lernaea cyprinacea	*Chanodichthys erythropterus*	Xenocyprididae	Dongxi Lake, China; Jingzhou, China	DQ107555	DQ107547	KM235194	Song *et al.* (2008) and Su *et al.* (2016)

Newly generated sequence is given in bold.

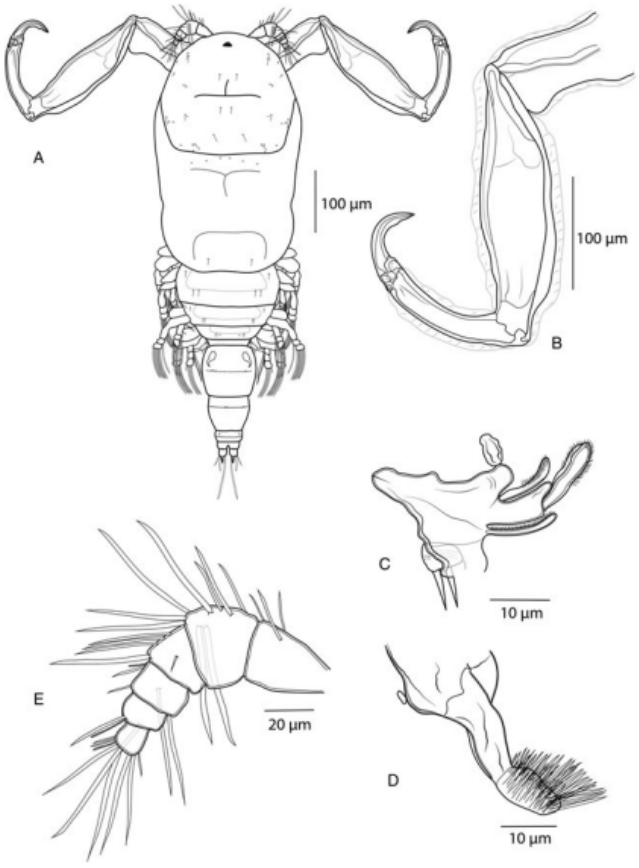


Figure 2. *Dermoergasilus madagascarensis* n. sp., adult female from *Paretroplus polyactis*. (A) habitus, dorsal; (B) antenna, ventral; (C) mandible and maxilulle, ventral (D) maxilla, ventral; (E) antennule, ventral.

Caudal rami nearly equal in length with AS-3, slightly wider than long; each projecting into tapering digitiform process (about 1.6 times longer than body of ramus) with inconspicuous terminal seta (Fig. 5E) and bearing 3 terminal setae – the innermost longest and thickest, ornamented with transversal rings of inconspicuous scales at posterior 3/4; 2 lateral setae longer than digitiform processes. Two cylindrical egg-sacs, much longer than wide (4 times), each composed of 2–4 rows of eggs (Fig. 3B).

Antennule (Figs 2E and 5C) 6-segmented, tapering, distally armed with simple setae; setal formula from proximal to distal segments: 3–9 – 5–4 + ae – 2 + ae – 7 + ae. Antenna (Figs 2B and 5B) comprising coxobasis, 3-segmented endopod (Enp-1 to Enp-3), and strongly recurved terminal claw. Enp-1 (proximal) longest, nearly 1.7 times longer than coxobasis, slightly inflated medially, unornamented; Enp-2 (medial) elongated, slightly curved, about half length of Enp-1, unornamented; ES-3 inconspicuous, unornamented. Terminal claw curved, about half size of ES-2, with inconspicuous subterminal inner denticle. Antenna (except terminal claw) covered with inflated cuticular membrane, without setules, spines or indentations.

Mouthparts (Fig 2C and D) comprising mandible, maxillule and maxilla; maxilliped absent. Mandible consisting of 3 blades (anterior, middle and posterior); anterior blade with sharp teeth on anterior margin; middle blade with sharp teeth on both margins; and posterior blade with sharp teeth on anterior margin. Maxillule a single lobe, ornamented with rows of tiny spinules, bearing 2 equally long outer setae and minute inner seta. Maxilla 2-segmented, comprising syncoxa and basis; syncoxa small, unarmed; basis elongated, medially slightly curved, distally with numerous sharp teeth on anterior side.

Swimming legs (L1–L4) biramous; each comprising coxa, basis, endopod (inner ramus), and exopod (outer ramus) (Fig. 4). Intercoxal sclerites slender; each with tapering ends directed posterolaterally, unornamented. Interpodal plates slender, uniform in shape; each with 2 inconspicuous bilateral pores and 3–4 transversal rows of spinules (Figs 3E and 5D). Armature formula of L1–L4 (spines – Roman numerals; setae – Arabic numerals) shown in Table 5.

Coxa of all legs unarmed; coxa of L1 with a row of spinules extending along its outer posterior margin. Basis of all legs armed with proximal outer spine, unornamented. Legs 1–4 with outer margin of both rami ornamented with rows of spinules; outer and inner margin of first endopodal and exopodal segment, respectively, of all legs partly or completely covered with bristles.

Leg 1 (Fig. 4A): exopod 3-segmented; first segment with small naked spine arising from outer posterior margin; second segment with inner plumose seta; third segment with 2 blade-like serrated spines (shorter more proximal), 1 semi-plumose seta (=seta with outer margin serrated) and 4 plumose setae.

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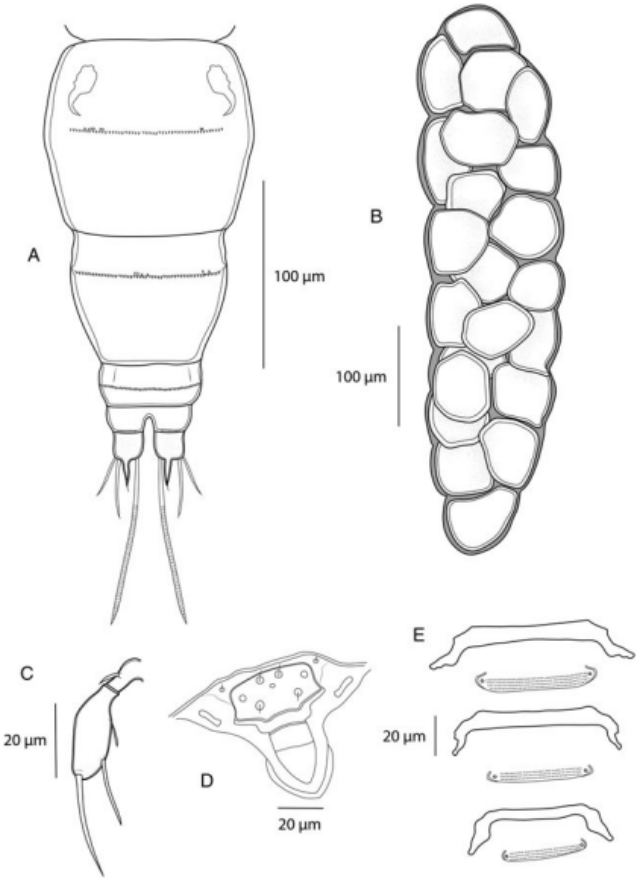


Figure 3. *Dermoergasilus madagascarensis* n. sp., adult female from *Paretroplus polyactis*. (A) abdomen and caudal rami; (B) egg sac, dorsal; (C) leg 5, ventral; (D) rostrum, dorsal; (E) interpodal plates, ventral.

Endopod 3-segmented; first and second segment each with 1 plumose seta; third segment with 3 plumose setae, 1 semi-plumose seta and 2 blade-like serrated spines.

Leg 2 (Fig. 4B): exopod 3-segmented; first segment with small outer spine; second segment with 1 plumose seta; third segment with 1 semi-plumose seta and 5 plumose setae.

Endopod 3-segmented; first and second segments each with 1 small slender serrated spine, 1 plumose seta; third segment with 3 plumose setae, 1 semi-plumose seta.

Leg 3 (Fig. 4C): exopod 3-segmented; first segment with small outer spine; second segment with 1 plumose seta; third segment with 1 semi-plumose seta and 5 plumose setae. Endopod 3-segmented; first and second segments each with 1 plumose seta; third segment with 1 small slender serrated spine, 3 plumose setae and 1 semi-plumose seta.

Leg 4 (Fig. 4D): exopod 2-segmented; first segment elongated, with small outer spine; second segment with 5 plumose setae. Endopod 3-segmented; first segment with 1 plumose seta; second segment with 2 plumose setae; third segment with 1 slender serrated spine and 3 plumose setae.

Leg 5 (Figs 3C and 5F): reduced but clearly visible, 2-segmented. Basal segment very small and visible dorsally, bearing outer seta; distal segment with 3 setae on inner margin (apical seta largest).

Specimens preserved in ethanol faint brown in colour, with blue spot in eyespot and sometimes in cephalothorax.

Male: Unknown

Remarks

Dermoergasilus madagascarensis n. sp. represents another species of *Dermoergasilus*, besides *D. curtus* (El-Rashidy and Boxshall, 2001) and *D. intermedius* (Kabata, 1992), that have antennae with only slightly inflated cuticular membrane. All other known *Dermoergasilus* spp. possess a conspicuous balloon-like inflated membrane covering all or only the first (in *D. semicoleus*) antennal endopodal segment. In *D. curtus*, however, the cuticular membrane covers only the inner surface of the first endopodal segment of the antenna, whereas in *D. intermedius* and *D. madagascarensis* n. sp. the membrane ensheathes all endopodal segments. The new species differs further from *D. curtus* mainly by having: (i) a pentagon-shaped cephalosome (*vs* bullet-shaped cephalosome); (ii) second endopodal segment of the antenna without a minute seta (*vs* with a minute seta proximally on inner margin of the segment); (iii) interpodal plates ornamented with 3–4 rows of spinules (*vs* 1 row of spinules); (iv) genital segment with 1 medial row of spinules (*vs* 3 posterior rows of spinules); (v) urosomites without folded membrane; and (vi) 2 lateral caudal setae longer than the digitiform

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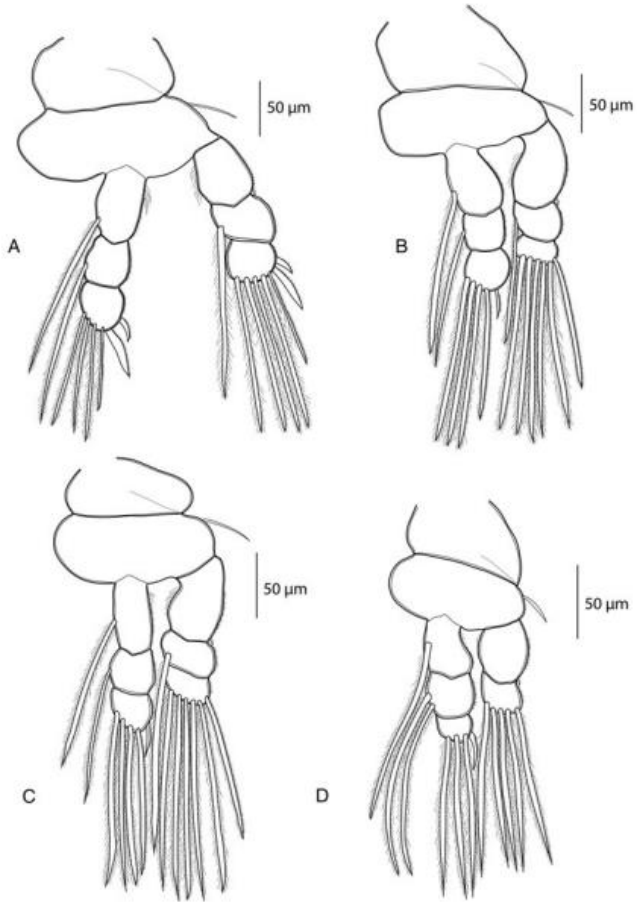


Figure 4. *Dermoergasilus madagascarensis* n. sp., adult female from *Paretroplus polyactis*. (A) leg 1, ventral; (B) leg 2, ventral; (C) leg 3, ventral; (D) leg 4, ventral.

process (*vs* shorter than the digitiform process). *Dermoergasilus madagascarensis* n. sp. is easily differentiated from *D. intermedius* by having: (i) anteriorly rounded and slightly tapering pentagonal cephalosome (*vs* anteriorly flat square-shaped cephalosome with widely separated antennules); (ii) second endopodal segment of the antenna medially swollen (*vs* the segment slender and of the same diameter along entire antenna); (iii) interpodal plates ornamented with 3–4 rows of spinules (*vs* unornamented); (iv) genital segment with 1 medial row of spinules (*vs* 1 posterior row of spinules, sometimes with gaps in middle part); (v) 2 lateral caudal setae longer than the digitiform processes (*vs* 1 longer and 1 shorter than the digitiform process); and (vi) a different armature formula of the third endpodal segment of legs II to IV.

In terms of the armature of the swimming legs, *D. madagascarensis* n. sp. shares the same spine and setal formula with 6 other species of *Dermoergasilus*, namely *D. amplectens*, *D. cichlidus*, *D. curtus*, *D. longiabdominalis*, *D. occidentalis* and *D. semiamplectens*, recorded on fishes of different families, but mostly of the Mugilidae (see Table 1). With the exception of *D. curtus*, all 5 species mentioned above are clearly distinguished from the new species by having a slender urosomite (genital segment and the first abdominal somite are markedly elongated *vs* both barrel shaped in *D. madagascarensis* n. sp.).

Dermoergasilus madagascarensis n. sp. is the first recorded copepod parasitizing freshwater fishes in Madagascar and besides *D. amplectens* from orange chromid *Pseudetroplus maculatus* (Bloch) (India; Ho *et al*., 1992) and *D. cichlidus* from *Coptodon zilii* (Iraq; Ali and Adday, 2019), it is the third species of *Dermoergasilus* hitherto recorded from the gills of a cichlid fish.

Molecular characterization and phylogenetic position of D. madagascarensis *n. sp. within the Ergasilidae*

Partial fragments of 18S (1384 bp), 28S (674 bp) rDNA and COI (675 bp) were obtained from 10 individuals of *D. madagascarensis* n. sp. No intraspecific sequence variability was found for any of nuclear ribosomal markers (partial 18S and 28S rDNA). Six haplotypes were found in the COI mtDNA with a low intraspecific genetic variation of 0.15–1.48%. Genetic comparison of *D. madagascarensis* n. sp. with other Ergasilidae species showed the lowest interspecific genetic distance with *Ergasilus megaceros* Wilson, 1916 (17.7%) and highest interspecific genetic distance with *Neoergasilus japonicus* (Harada, 1930) (23.9%) for COI sequences (Table 6). When comparing *D. madagascarensis* n. sp. to other ergasilid species in rDNA sequence data, the minimum interspecific distances were observed with *E. sieboldi* von Nordmann, 1832 (0.9% for 18S rDNA, and 4.3% for 28S rDNA) and maximum interspecific divergences were observed with *Therodamas longicollum* Oliveira *et al.*

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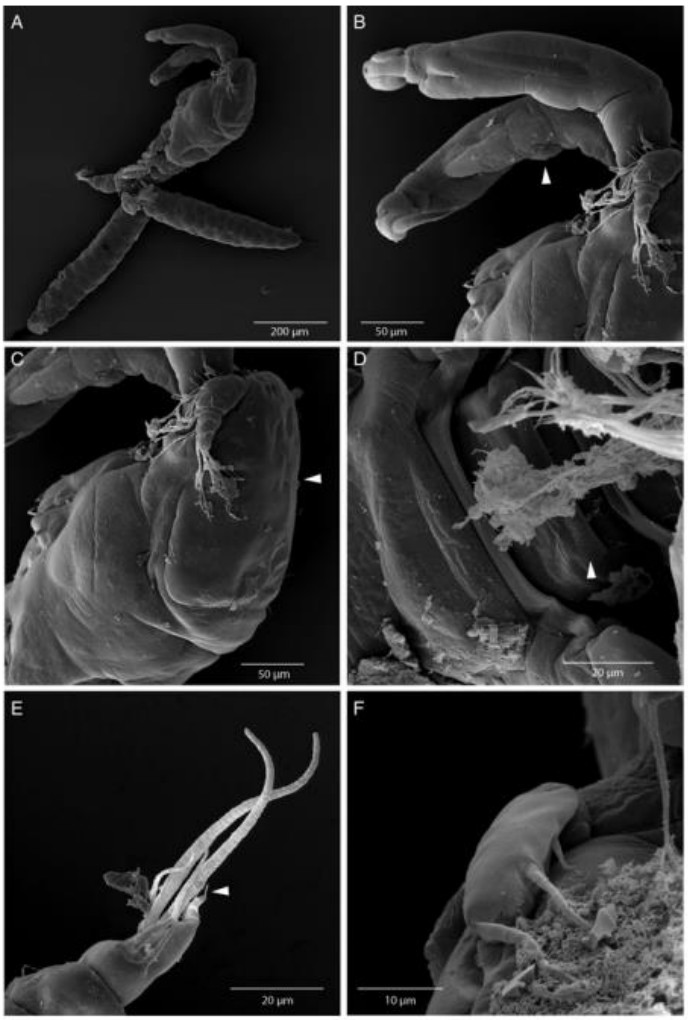


Figure 5. Scanning electron micrographs of *Dermoergasilus madagascarensis* n. sp., adult female from *Paretroplus polyactis*. (A) entire female body, carrying egg sacs, lateral; (B) antenna with transparent membrane (arrow), dorsal; (C) cephalosome with sensory setae and pits (arrow); antennule, lateral dorsal; (D) interpodal plates with ornamentation (arrow), ventral; (E) caudal rami and digitiform process (arrow), ventral; (F) leg 5, ventral.

(2021) (3.4% for 18S rDNA) and *Sinergasilus major* (Markevich, 1940) (10.9% for 28S rDNA).

ML and BI analyses based on 28S rDNA sequences of Ergasilidae yielded trees with congruent topologies with similar nodal support values and revealed 5 well-supported groups (Fig. 6): (A) African *Ergasilus* species group; (B) Asian *Sinergasilus* species and the *Ergasilus anchoratus* Markevich, 1946 group; (C) Asian *Ergasilus* species and the *Neoergasilus japonicus* group, (D) *E. sieboldi* and *D. madagascarensis* n. sp. group and (E) *Paraergasilus* species and the *Ergasilus wilsoni* Markevich, 1933 group. Phylogenetic reconstruction showed the polyphyletic status of the genus *Ergasilus*.

Discussion

Diversity of fish ectoparasites in native Malagasy freshwater fish has been little studied in the past. The present study was a part of large parasitological investigation performed only in 4 localities of north-western Madagascar, however, documenting unknown diversity of fish parasites in isolated freshwater region with endemic fish fauna (i.e., Madagascar), the pattern which was previously shown for endemic freshwater fish in other regions i.e., Peri-Mediterranean and Middle East (Benovics *et al.*, 2017, 2021; Rahmouni *et al.*, 2017; Řehulková *et al.*, 2020; Nejat *et al.*, 2023). Prior to this study, 12 valid species of *Dermoergasilus* were known, including 1 species, specifically *D. longiabdominalis*, in mugilid hosts in Madagascar. Two *Dermoergasilus* species were previously reported on cichlid hosts in India and Iraq. The first species, *D. amplectens*, was recorded on a number of fish species and over a wide geographic range, including *Pseudetroplus maculatus*, an endemic cichlid of southern India and Sri Lanka. The second species, *D. cichlidus*, was described from *Coptodon zillii*, a non-native cichlid in Iraq. *Dermoergasilus madagascarensis* n. sp. represents the third species of the genus reported on

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Table 4. Measurements (in micrometers) of specimens ($n = 10$) of *Dermoergasilus madagascarensis* n. sp. parasitizing endemic cichlid *Paretroplus polyactis* in Madagascar

Character	Range	Mean
Total length	610–754	695
Body width	207–239	223
Cephalosome length	207–253	226
Cephalosome width	210–266	234
Antennule length	105–118	110
Antenna length	474–509	485
Antennal segment 1 length	105–135	117
Antennal segment 2 length	180–215	198
Antennal segment 3 length	106–117	112
Antennal segment 4 (claw) length	52–66	57
Cephalothorax length	352–371	364
Cephalothorax width	238–294	260
Thoracic segment 2 length	51–61	57
Thoracic segment 2 width	145–167	157
Thoracic segment 3 length	38–48	43
Thoracic segment 3 width	104–118	112
Thoracic segment 4 length	30–34	32
Thoracic segment 4 width	75–79	77
Thoracic segment 5 length	13–18	17
Thoracic segment 5 width	58–77	67
Genital double somite length	79–95	88
Genital double somite width	84–100	92
Abdominal segment 1 length	42–62	50
Abdominal segment 1 width	56–73	66
Abdominal segment 2 length	18–23	20
Abdominal segment 2 width	45–55	51
Abdominal segment 3 length	15–18	16
Abdominal segment 3 width	36–46	43
Caudal ramus length	14–16	15
Caudal ramus width	15–20	17
Egg-sac length	420–589	519
Egg-sac width	112–125	118

cichlids and the second species of the genus revealed in Madagascar and a single known species currently known only from endemic Malagasy cichlids (i.e., *P. polyactis*).

Even though questioned in the past (Gussev, 1987; Kabata, 1992; El-Rashidy and Boxshall, 2001), *Dermoergasilus* still remains valid. From the 3 morphological characters proposed by Ho and Do, 1982 only 1 clearly differentiates this genus, which is a digitiform process on each paired caudal rami. The other 2 characters seem to be ambiguous. The inflated transparent membrane is quite a vague morphological character, and some species of *Dermoergasilus* do not have it well developed (e.g. *D. curtus* or *D. intermedius*). The membrane could be an ancestral trait that is being lost during the evolution, from clearly visible balloon-like inflation in *D. amplectens* to barely noticeable cuticle in *D. curtus*. Moreover, there are some *Ergasilus* species with some kind of hyaline membrane on antenna. For example, the membrane on antenna of *Ergasilus megacheir* (Sars, 1909) appears to be very similar to that of *D. curtus*. The middle segment of endopod of legs II and III possessing a single seta is even less persuasive character, since at least 10 *Ergasilus* species (e.g. *E. tumidus* Markevich, 1940, *E. briani* Markevich, 1933, *E. gibbus* von Nordmann, 1832, *E. gobiorum* Markevich & Sukhnenko, 1967 etc.) also possess this character (Ho *et al.*, 1992; Kabata, 1992). There are other morphological traits present in most of the species of *Dermoergasilus*, e.g. long first free abdominal segment, similar morphology of leg 5, falciform seta on legs, some species even share the same spine-seta and antennal formula. However, neither of them can clearly distinguish *Dermoergasilus* from other members of Ergasilidae but could indicate their possible close relationship and a common ancestry.

Table 5. Spine (Roman numerals) and setal (Arabic numerals) formula of swimming legs of *D. madagascarensis* n. sp.

	Coxa	Basis	Exopod	Endopod
Leg 1	0–0	1–0	I-0; 0–1; II-5	0–1; 0–1; II-4
Leg 2	0–0	1–0	I-0; 0–1; 0–6	0–1; 0–1; I-4
Leg 3	0–0	1–0	I-0; 0–1; 0–6	0–1; 0–1; I-4
Leg 4	0–0	1–0	I-0; 0–5	0–1; 0–2; I-3

Based on the literature review, *D. madagascarensis* n. sp. shares the same spine and setal formula with 6 other species of the genus. Future studies using molecular analyses should focus on this aspect and verify, if species with the same armature of swimming legs are phylogenetically related. Many of these species were recorded from mugilid hosts in Indian region. It is possible that they have the common origin, and the divergence of the species is associated with geographical isolation of Madagascar, drifting away from the Indian peninsula 96–65 Mya (Vences *et al.*, 2009). El-Rashidy and Boxshall (2001) suggested that a mugilid as a host is a plesiomorphic character for *Dermoegasilus*, and that the ancestor of this group of parasites also occurred on a mugilid host. Acquiring hosts of other fish families could be a result of the adaption to the conditions in the new environment, which are cichlids in this case. However, only molecular data from *D. curtus*, *D. longiabdominalis* and *D. semiamplectens* reported from mugil hosts in India, China, Madagascar, Philippines and Myanmar would shed more light on the origin of *D. madagascarensis* n. sp. and clarify its relationship with other *Dermoergasilus* and *Ergasilus* species.

Scanning electron microscopy (SEM) is the method providing the appropriated visualization of some morphological structures, in our study, specifically sensory setae and pits, and also the minute seta on the digitiform process in *D. madagascarensis* n. sp., while the latter character was not visible under the light microscope. It is highly likely that some morphological characters might be overlooked in older descriptions of Ergasilidae, in which authors did not use SEM.

The present results of phylogenetic analyses are consistent with previously reported ergasilid phylogenies (Song *et al.*, 2008; Santacruz *et al.*, 2020; Kvach *et al.*, 2021; Míč *et al.*, 2023). Phylogenetic reconstruction based on 28S rDNA presented in this study showed the sister relationship among newly described *D. madagascarensis* n. sp. and *E. sieboldi* von Nordmann, 1832, a cosmopolitan parasite of freshwater fishes (Yamaguti, 1939; Kabata, 1979; Amado *et al.*, 2001). While the cephalothorax shape is similar between the 2 species, the new species differs from *E. sieboldi* by: (i) digitiform process on caudal rami (ii) absence of spines on antenna (*vs* short spine on inner surface of the first endopodal segment of antenna and 2 short spines on inner surface of the second endopodal segment of

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Table 6. Interspecific genetic variabilities of family Ergasilidae

		1	2	3	4	5	6	7	8	9	10
1	***Dermoergasilus* (1, 1, 1)**		**21.3–22.4**	**17.7–23.6**	**20.8–23.9**	–	**19.5–22.1**	**20.6–21.2**	**21.4–22.1**	**22.4–23.0**	–
2	*Acusicola* (1, 1, 1)	**2.1**		16.7–22.9	17.4–18.4	–	18.4–20.4	20.8–21.8	20.6–21.6	20.9–21.6	–
		5.8									
3	*Ergasilus* (13, 14, 11)	**0.8–2.7**	1.6–3.0		18.1–21.9	–	16.4–22.0	17.1–21.2	20.5–23.8	19.5–24.8	–
		4.3–9.6	5.3–9.9								
4	*Neoergasilus* (1, 1, 1)	**1.6**	1.9	0.5–2.0		–	17.3–20.1	20.1–21.2	19.9–20.6	20.9–21.5	–
		7.5	8.9	5.6–11.2							
5	*Paraergasilus* (3, 3, 0)	**1.6–1.9**	2.3–2.4	1.2–3.0	2.1–2.3		–	–	–	–	–
		5.4–6.1	5.5–6.0	3.5–9.4	7.2–7.5						
6	*Sinergasilus* (3, 3, 2)	**1.7–2.1**	1.7–1.9	0.5–2.8	1.6–1.7	2.1–2.4		18.8–19.5	19.1–21.6	20.6–21.4	–
		8.8–10.9	9.6–11.4	8.0–12.6	11.0–12.6	8.6–10.9					
7	*Gammispinus* (1, 0, 1)	**1.5**	1.9	1.4–3.3	1.5	2.0–2.4	2.0		20.8–21.4	23.1	–
		–	–	–	–	–	–				
8	*Miracetyma* (1, 0, 1)	**2.4**	2.3	1.9–4.4	3.1	2.7	3.1	2.7		26.0–26.3	–
		–	–	–	–	–	–	–			
9	*Paeonodes* (0, 0, 1)	–	–	–	–	–	–	–	–		–
		–	–	–	–	–	–	–	–		
10	*Therodamas* (1, 0, 0)	**2.9**	2.9	1.8–3.9	2.9	2.7	2.7	3.7	3.4	–	
		–	–	–	–	–	–	–	–		

Below the diagonal are showed the values for 18S rDNA (first line) and 28S rDNA(second line) and above the diagonal for COI. The range indicates minimum and maximum value of the genetic variability for species of the genus. Numbers in brackets indicate the number of species with available sequences for the specific marker (18S, 28S, COI). Bold numbers only indicate values for the genus *Dermoergasilus*, which is the focus of this article.

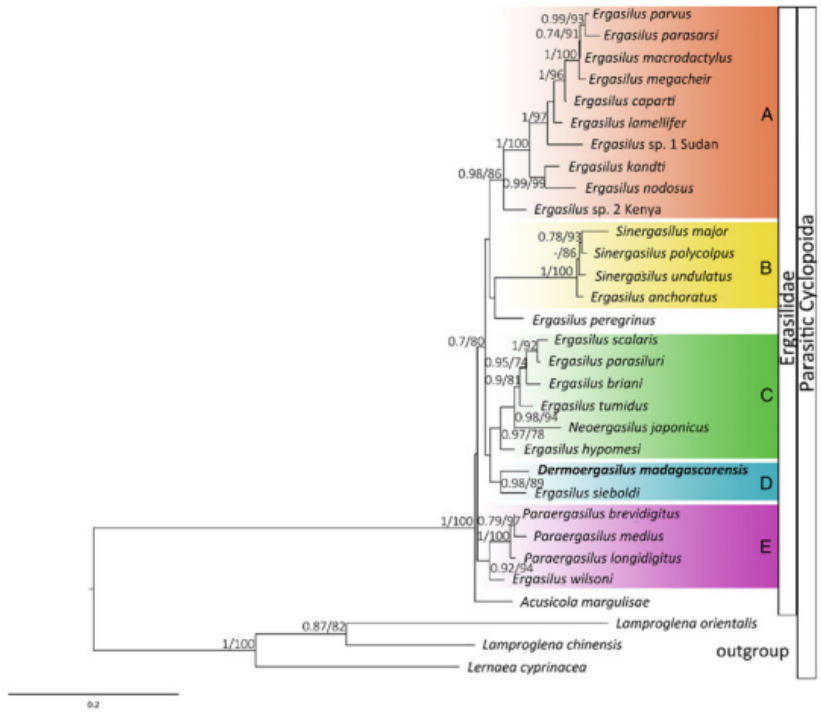


Figure 6. Phylogenetic tree of Ergasilidae reconstructed by Maximum Likelihood. The tree is based on the partial 28S rDNA sequences (674 bp alignment). Values along the branches indicate posterior probabilities from Bayesian Inference and bootstrap values from Maximum Likelihood (dashes indicate values below 0.7 and 50, respectively).

antenna in *E. sieboldi*); (iii) absence of circular structure posterior to inverted T-structure on cephalothorax (*vs* presence in *E. sieboldi*), (iv) caudal rami bearing 3 terminal setae (*vs* 4 terminal setae in *E. sieboldi*); (v) having only 1 seta on the second segment of the endopods of legs II and III (*vs* 2 setae in *E. sieboldi*).

However, we can still ask whether the position of *D. madagascarensis* n. sp. in the phylogenetic tree is because of the real relatedness of these 2 species or due to the lack of molecular data for other species of the family Ergasilidae, especially those currently included in *Dermoergasilus*. A close relationship among *D. madagascarensis* n. sp. and African species of *Ergasilus* has not been confirmed in present study, so the newly described species does not appear to originate from Africa (at least based on the phylogeny including currently available DNA sequences of African *Ergasilus*). A fragment of COI mtDNA gene was also successfully obtained for representative number of *D. madagascarensis* n. sp. specimens. Unfortunately, no other DNA data are currently available for representatives of the *Dermoergasilus* genus and no threshold for intra- or interspecific variability was set for ergasilid species. However, the distances between COI haplotypes of *D. madagascarensis* n. sp. did not exceed 1.5%, the intraspecific limit generally accepted for COI mtDNA of Copepoda (Bucklin *et al.*, 2003; Dippenaar *et al.*, 2010; Laakmann *et al.*, 2013). The COI intraspecific distances in other ergasilid species reached the values from 0% (*E. wilsoni* or *E. jaraquensis* Thatcher & Robertson B.A., 1982) to 6.9% (*N. japonicus*). In contrast, COI distances between *Dermoergasilus* and other genera reached values over 17%, supporting it being a separate genus. Nevertheless, to clearly resolve the phylogeny of Ergasilidae, DNA sequences of more ergasilid species from other parts of the world are needed.

Conclusion

Based on morphological and molecular data, a new species of *Dermoergasilus* has been described. *Dermoergasilus madagascarensis* n. sp. from the cichlid *P. polyactis* is the second report of a representative of the genus in Madagascar and the first molecular data for the genus were obtained. Even though the validity of the genus was questioned in the past, the possession of digitiform process on caudal rami clearly distinguishes it from other genera of the Ergasilidae. However, our phylogenetic analyses showed the polyphyly of the genus *Ergasilus*, and the close phylogenetic relationship between *D. madagascarensis* n. sp. and widely geographically distributed *Ergasilus sieboldi*. We highlight that more molecular data are needed to clarify the relationships between the species of *Dermoergasilus* and their position within the Ergasilidae.

Supplementary material. The supplementary material for this article can be found at https://doi.org/10.1017/S0031182024000088.

Data availability statement. Type and voucher specimens were deposited in the Institute of Parasitology, Czech Academy of Sciences, České Budějovice, Czech Republic (accession code Cr-39). The sequences produced in this study were deposited in GenBank of NCBI at https://www.ncbi.nlm.nih.gov/ (accession codes PP115568, PP115569, PP117929-PP117934).

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Authors' contributions. AŠ, RM and MS conceived and designed the study. EŘ and AŠ collected parasitological material, RM performed morphological characterization and described the species. RM and MS performed molecular and phylogenetic analyses. RM and MS wrote the first draft of the manuscript, EŘ reviewed description of the species. All authors substantially contributed to the final draft and approved the final version of the manuscript.

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Competing interests. None.

Ethical standards. All applicable institutional, national and international guidelines for the care and use of animals were followed. The fish sampling was carried out following permission No. 06/AR.ED./15 issued on April 1, 2016 by the General Directorate for Fishery Resources and Fisheries, Ministry of Fisheries Resources and Fisheries, Madagascar..

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Paper 3

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Diversity and phylogeny of parasitic copepods of freshwater fishes from the Mediterranean and the Middle East

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Abstract

The Mediterranean and the Middle East represent unique biogeographical regions that significantly shaped the evolutionary history and particular diversity of their associated organisms. However, knowledge on the copepods parasitizing freshwater fishes in these regions is limited. This study aims to investigate the diversity and phylogeny of parasitic copepods in freshwater fishes across the Mediterranean and the Middle Eastern regions. A total of 169 freshwater fish species from the Mediterranean and Middle East were examined for metazoan parasites, yielding over 1000 parasitic copepods. A thorough morphological evaluation combined with molecular analyses of partial fragments of rDNA (18S and 28S) and mitochondrial cytochrome c oxidase subunit I (COI) led to the identification of 7 species of Ergasilidae and 3 species of Lernaeidae. These findings include the descriptions of 2 new species: *Ergasilus italicus* n. sp. parasitizing South European nase, *Protochondrostoma genei* (Bonaparte, 1839), in Italy and *Pseudolamproglena zahrziensis* n. sp. found in yellow barbel, *Carasobarbus luteus* (Heckel, 1843), in Iraq. New host and geographical records, along with molecular data are provided for 8 previously described species – *Ergasilus barbi* Rahemo, 1982, *Ergasilus briani* Markevich, 1933, *Ergasilus lizae* Krøyer, 1863, *Ergasilus rostralis* Ho, Jayarajan & Radhakrishnan 1992, *Neoergasilus japonicus* (Harada, 1930), *Paraergasilus longidigitus* Yin, 1954, *Lamproglena pulchella* von Nordmann, 1832 and *Lernaea cyprinacea* Linnaeus, 1758.

Introduction

Freshwater parasitic copepods, particularly members of the Ergasilidae and Lernaeidae, are significant pathogens and vectors of fish diseases, impacting fish population dynamics and health (Boxshall and Defaye, 2008; Boxshall and Hayes, 2019). Despite their ecological importance, these parasites remain relatively understudied, and their role in aquatic ecosystems is still not completely clarified. Current knowledge of their diversity varies regionally due to inconsistent research efforts.

Within the Palearctic realm, the Mediterranean and the Middle East are biogeographical regions, each defined by its unique combination of climatic, geological and hydrological conditions that have shaped the evolution and diversity of organisms living in these areas. Both regions are recognized for their high level of biodiversity and endemism, which has long attracted scientific interest (Cuttelod et al., 2009; Freyhof et al., 2014, 2021). However, research on parasitic copepods of the Ergasilidae and Lernaeidae in these regions remains limited and rather uneven. More extensive studies, including the descriptions of new species (*Dermoergasilus cichlidus* Ali and Adday, 2019; *Ergasilus luteusi;* Al-Sahlany et al., 2024; *Pseudolamproglena boxshalli*; Al-Nasiri et al., 2012) in recent years (Al-Nasiri et al., 2012; Ali and Adday, 2019; Al-Sahlany et al., 2024), have been conducted only in a few countries, mainly in Turkey (e.g. Soylu and Soylu, 2012; Koyun et al., 2015; Öktener, 2021) and Iraq (e.g. Mhaisen and Abdul-Ameer, 2021; Mhaisen and Al-Daraji, 2023). In the Mediterranean, particularly in its European part, research on parasitic copepods is also limited to specific regions, several studies were conducted in Bosnia and Herzegovina (Nedić et al., 2014; Skenderović et al., 2015, 2021), Croatia (Tomašec, 1953; Fijan, 1974, 1982), Greece (Zarfdjian and Economidis, 1989; Ragias et al., 2005), Spain (e.g. Simon Vicente et al., 1973; Almeida et al., 2008), Portugal (e.g. Hermida et al., 2008; Bao et al., 2016) and Italy (Grandori, 1925; Fratello and Sabatini, 1972; Macchioni et al., 2015). However, most of these studies do not represent comprehensive research integrating both morphological and molecular approaches, and parasitic copepods have often also remained unidentified (Saraiva and Valente, 1988; Vagianou et al., 2006; Nedić et al., 2014; Stamou et al., 2022).

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Until now, 30 species belonging to 6 genera of Ergasilidae [*Dermoergasilus* Ho & Do, 1982 (3), *Ergasilus* von Nordmann, 1832 (19), *Mugilicola* Tripathi, 1960 (2), *Nipergasilus* Yamaguti, 1939 (1), *Neoergasilus* (Yin, 1956) (2) and *Paraergasilus* Markevich, 1937 (3)) and 10 species belonging to 3 genera of Lernaeidae (*Lamproglena* von Nordmann, 1832 (5), *Lernaea* Linnaeus, 1758 (3) and *Pseudolamproglena* (Boxshall, 1976) (2)] have been recorded in the Mediterranean and Middle East regions. A detailed checklist of all records of species of the Ergasilidae and Lernaeidae in the Mediterranean and the Middle East is provided in Supplementary Table S1.

Within the Ergasilidae, *Ergasilus* is currently the most abundant and diverse genus, with up to 19 species reported in these areas. The most widespread species is *Ergasilus sieboldi* von Nordmann, 1832, which has been reported from various freshwater hosts from the Iberian Peninsula to Iraq. In contrast, other *Ergasilus* species have shown more restricted distributions (e.g. *Ergasilus boleophthalmi* Adday & Ali, 2011; *Ergasilus iraquensis* Amado in Amado, da Rocha, Piasecki, Al-Daraji & Mhaisen, 2001; *Ergasilus luteusi* Al-Sahlany et al., 2024; *Ergasilus pararostralis* Amado in Amado, da Rocha, Piasecki, Al-Daraji & Mhaisen, 2001 and *Ergasilus synanciensis* Amado in Amado, da Rocha, Piasecki, Al-Daraji & Mhaisen, 2001 are all restricted to Iraq) or greater host specialization, such as *Ergasilus gibbus* von Nordmann, 1832, which predominantly parasitizes fishes from the family Anguillidae. From the genus *Neoergasilus* have been recorded 2 species, *Neoergasilus longispinosus* (Yin, 1956) on cyprinids in Algeria (Boucenna et al., 2018; Berrouk et al., 2020, 2022) and *Neoergasilus japonicus*, a globally invasive species (Ondračková et al., 2024) of various fish families, has been recorded in several countries in both regions (e.g. Soylu and Soylu, 2012; Mirzaei et al., 2016; Berrouk et al., 2022). Three species of *Paraergasilus* (*Paraergasilus brevidigitus* Yin, 1954; *Paraergasilus inflatus* Ho et al., 1996 and *Paraergasilus longidigitus* Yin, 1954) were recorded in Iraq, Algeria and Turkey (Ho et al., 1996; Koyun et al., 2007; Berrouk et al., 2022). In addition, an introduced non-native species, *Nipergasilus bora* (Yamaguti, 1939), has been recorded on fish hosts of the family Mugilidae in several Mediterranean countries (Paperna, 1975; Ben Hassine, 1983; Koyun et al., 2007). Two species of *Mugilicola* (*Mugilicola bulbosa* Tripathi, 1960 and *Mugilicola kabatai* Piasecki et al., 1991) parasitizing on fishes of the family Mugilidae and 3 species of *Dermoergasilus* (*Dermoergasilus amplectens* (Dogiel & Akhmerov, 1952), *D. cichlidus* and *Dermoergasilus varicoleus* Ho et al., 1992) found on a variety of fish species were reported only in Iraq (Piasecki et al., 1991; Ho et al., 1996; Amado Pinto da Motta et al., 2001; Ali and Adday, 2019; Al-Mosawi and Adday, 2024).

Within the Lernaeidae, 5 species of the genus *Lamproglena* have been recorded, but only *L. pulchella* was found in Europe, with its distribution extending as far as Iraq (Mhaisen et al., 2024). Other *Lamproglena* species, *Lamproglena chinensis* Yü, 1937; *Lamproglena compacta* Markevich, 1936 and *Lamproglena jordani* (Paperna, 19640 have been recorded on the Cyprinidae and Leuciscidae in Iraq, Iran and Israel, respectively, while *Lamproglena monodi* Capart, 1944 was recorded on Cichlidae in Egypt (e.g. 1964; Pazooki and Masoumian, 2012; Hassan et al., 2013). The genus *Lernaea* is predominantly represented by the invasive cosmopolitan species *L. cyprinacea*, which is distributed in almost all Mediterranean and Middle Eastern countries (Ondračková et al., 2024). Additionally, two other species, *Lernaea ctenopharyngodontis* Yin, 1960 and *Lernaea oryzophila* Monod, 1932, have been recorded from cyprinid hosts

Table 1. List of sampled localities with coordinates (only positive records of parasitic copepods listed, all localities are listed in Supplementary Table S2)

Country	ID	Locality	Coordinates
Portugal	P4	Colares	38°47′53.37″N 09°26′14.16″W
	P6	Torgal river, Mira basin	37°38′16.76″N 08°37′10.58″W
Spain	S2	Magro river (1)	39°21′25.76″N 00°39′51.76″W
	S3	Magro river (2)	39°21′18.85″N 00°40′38.85″W
	S4	Turia river	39°34′46.46″N 00°37′09.63″W
	S7	Peraleda de Zaucejo, Zujar river	38°27′12.02″N 05°31′59.67″W
Italy	I3	Torrente Cerfone, Intoppo	43°26′12.03″N 11°58′33.00″E
	I4	Torrente Cerfone, Le Ville	43°28′42.00″N 12°04′25.03″E
	I8	Carmagnola, Cave Germaire	44°51′42.96″N 07°40′26.33″E
Croatia	C1	Baštica river, below the Baštica reservoir/Grabovač reservoir	44°11′42.37″N 15°24′32.13″E
	C8	Pazin, Pazinčica river	45°14′47.92″N 13°58′10.66″E
Bosnia and Herzegovina	BIH1	Krenica lake, Drinovci	43°22′25.00″N 17°19′59.04″E
	BIH3	Mušnica, Avtovac	43°08′42.05″N 18°35′45.00″E
	BIH6	Šujica, Šujičko Polje	43°49′41.43″N 17°10′48.20″E
	BIH15	Rečina river, near Jelim lake, Hutovo Blato	43°03′39.72″N 17°48′29.30″E
	BIH16	Zagorje, Jabuke	43°32′18.53″N 17°12′34.28″E
Albania	A7	Osum, Vodice	40°24′13.07″N 20°39′04.04″E
	A11	Skadar lake, Shiroke	42°03′24.94″N 19°28′07.05″E
Greece	G3	Gallikos, Mandres, Gallikos basin	40°52′07.33″N 22°53′59.12″E
	G5	Angistis, between Alistrati & Drama	41°05′42.08″N 24°00′18.29″E
	G7	Sperchios, Ypati	38°54′14.33″N 22°17′30.22″E
	G16	Acheron, Gliki	39°19′00.05″N 20°36′04.03″E
	G17	Kokitos, Pagrati	39°26′53.02″N 20°30′03.06″E
	G19	Trichonis lake, Panetolio	38°35′20.19″N 21°28′02.68″E
	G20	Aoos, Kalithea	40°01′16.67″N 20°41′40.19″E

(*Continued*)

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Table 1. (*Continued.*)

Country	ID	Locality	Coordinates
	G21	Macropotamos river, Filiouri basin	41°04′13.00′′N 25°32′52.00′′E
	G23	Yliky Lake	38°25′47.82′′N 23°14′37.09′′E
	G26	Zagoritikos River, Baldouma	39°41′46.28′′N 20°59′46.00′′E
	G27	Aoos	40°01′31.39′′N 20°41′48.75′′E
Iraq	IRQ1	Dukan Lake	36°10′12′′N 44°57′24′′E
	IRQ2	Great Zab River (1)	36°16′25′′N 43°38′40′′E
	IRQ3	Darbandikhan Lake	35°07′17′′N 45°43′50′′E
	IRQ7	Wadi Kalat Shirah, tributary of Tabin River	35°47′3′′N 44°58′43′′E
	IRQ8	Kani Shok, tributary of Tabin River	35°50′01′′N 45°06′16′′E
	IRQ9	Zahrzi, Tabin River	35°48′32′′N 45°01′20′′E
	IRQ10	Grdi Go, Zalm Stream	35°18′26′′N 45°58′18′′E
	IRQ11	Du Choman, Aw-e Shiler River	35°45′49′′N 45°27′12′′E
Turkey	TUR1	Çine River, near Çiftlikköy	37°45′48′′N 27°50′03′′E
	TUR3	Kocaalam Deresi	36°57′12′′N 28°17′13′′E
	TUR4	Çine River, near Sitmalik	37°24′36′′N 28°06′49′′E
	TUR6	Çifteler	39°20′40.2′′N 31°18′44.8′′E
	TUR7	Seyitgazi	39°21′27.5′′N 30°35′37.0′′E
	TUR8	Kütahya	39°22′48.8′′N 30°03′58.9′′E
	TUR15	Ardahan, Kura	41°06′56.9′′N 42°42′02.5′′E
	TUR17	Yiğitkonağı closest village, Çakir, Kura Basin	40°58′00.6′′N 42°35′15.9′′E
	TUR18	Ölçek, Ölçeksuyu, Kura Basin	41°08′01.4′′N 42°51′21.7′′E
	TUR21	Kayacik, Cuma stream, Euphrates Basin	39°53′45′′N 43°10′34′′E
	TUR25	Near Meydan village, inflow of Garzan river, Tigris Basin	38°21′19′′N 41°46′48′′E
	TUR26	Sinanköy, Akçayır stream (inflow of Batman river), Tigris Basin	37°51′56′′N 40°59′21′′E
	TUR33	ca 5 km north of Borçka, inflow of Çoruh, Çoruh Basin	41°24′13′′N 41°41′47′′E
	TUR37	Simav river, Karacabey	40°11′50.526′′N 28°21′12.321′′E
	TUR39	Sasal stream, Kuner	38°11′58.017′′N 27°8′9.305′′E
	TUR53	Büyük Menderes, around 1 km east of Işıklı lake	38°12′49.74′′N 29°49′16.83′′E

(*Continued*)

in Iran and Iraq, respectively (Al-Nasiri et al., 2001; Pazooki and Masoumian, 2012). The genus *Pseudolamproglena* is absent in Europe, but 2 species (*Pseudolamproglena annulata* Boxshall, 1976 and *Pseudolamproglena boxshalli;* Al-Nasiri et al., 2012) were recorded on Cyprinidae, Leucisdidae and Mugilidae in Iraq (Boxshall, 1976; Al-Nasiri et al., 2012).

In this study, we provide an updated overview of the parasitic copepod fauna in freshwater fish species from the Mediterranean and the Middle Eastern regions. The research is based on extensive sampling conducted from 2014 to 2023. This comprehensive dataset offers new insights into the diversity, distribution and host associations of parasitic copepods in these areas, filling important gaps in the current knowledge.

Materials and methods

Fish collection

During several parasitological surveys between 2014 and 2023, 169 fish species (1484 specimens) were examined for the presence of metazoan parasites. Examined fish included mainly representatives of the Cyprinidae and Leuciscidae (total of 162 species), several fishes of the other families living in sympatry with cyprinoids were also examined (3 species of Gobionidae, 2 species of Nemacheilidae, 1 species of Cobitidae and 1 species of Mugilidae). Fishes were sampled in 155 localities including Spain (13 localities), Portugal (7 localities), Italy (8 localities), Croatia (15 localities), Bosnia and Herzegovina (11 localities), Albania (11 localities), Greece (27 localities), Turkey (52 localities) and Iraq (11 localities) (see Table 1 and Figure 1; for detailed information see Supplementary material Table S2 and Figure S1).

The fish sampling was carried out following local regulations. All applicable institutional, national and international guidelines for the care and use of animals were followed. All fish specimens were transported alive to the field laboratory, sacrificed by severing the spinal cord, and dissected within 48 hours following the classical parasitological dissection procedure (Scholz et al., 2018). All fish species used in this study were originally collected and previously used for the studies of monogenean parasites including molecular identification of fish (cytochrome *b*) (see Šimková et al., 2017; Benovics et al., 2018, 2020, 2021a, 2021b, 2021c, 2023, 2024; Nejat et al., 2023, 2025; Rahmouni et al., 2023). All fish sampling and morphological identification in the field was performed by the members of Czech team (Radek Šanda and Jasna Vukić) with contribution of local coworkers in all countries, their names are included in acknowledgements. The present study was part of a larger project concerning host-parasite relationships between monogeneans and their cyprinoid hosts.

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Figure 1. Map of sampling localities with records of parasitic copepods. (P – Portugal, S – Spain, I – Italy, C – Croatia, BIH – Bosnia and Herzegovina, A – Albania, G – Greece, TUR – Turkey, IRQ – Iraq).

Table 2. List of primers and PCR conditions used for DNA amplification of partial fragments of ribosomal genes (18S and 28S rDNA) and partial mitochondrial cytochrome oxidase gene (COI) of parasitic copepods

DNA fragment	Primer name	Direction	Sequence (5´–3´)	PCR thermal profile	Product size (bp)	Reference
18S rDNA	18SF	Forward	AAG GTG TGM CCT ATC AAC T	94 °C, 5 min; 40× (94°C, 30 s; 54°C, 30 s; 72°C, 1 min); 72°C, 5 min	~1300	Song et al. (2008)
	18SR	Reverse	TTA CTT CCT CTA AAC GCT C			
28S rDNA	28SF	Forward	ACA ACT GTG ATG CCC TTA G	94°C, 5 min; 40 × (94°C, 30 s; 54°C, 30 s; 72°C, 1 min); 72°C, 5 min	~650	Song et al. (2008)
	28SR	Reverse	TGG TCC GTG TTT CAA GAC G			
CO1 mtDNA	ergLCO-modif	Forward	AAYCAYAARGATATTG GNAC	95 °C, 5 min; 40 × (94 °C, 60 s; 45 °C, 60s; 72 °C, 60s); 72 °C, 7 min	~650	Present study
	ergHCO-modif	Reverse	GGRTGACCRAAAAAYC ARAA			

Parasite collection and identification

Live copepods were collected from the gills using fine needles and processed for morphological and molecular purposes, as described in Míč et al. (2023). The mounted specimens in GAP (mixture of glycerine and ammonium picrate) or pure glycerine were studied using an Olympus BX61 microscope equipped with phase contrast optics. Drawings of the copepods were made using an Olympus drawing attachment and edited with a graphic tablet (Wacom Intuos5 Touch) compatible with Adobe Illustrator and Adobe Photoshop (Adobe Systems Inc., San Jose, CA, USA). All measurements (in micrometres) were taken using digital image analysis software (Olympus Stream Motion v. 1.9.3) and are presented as the mean followed by the range and the number (*n*) of specimens measured in parentheses.

For scanning electron microscope analysis, two specimens fixed in 70% ethanol were dehydrated in an increasing ethanol grades, dried in a CPD 030 critical point drying apparatus (Baltec, Balzers, Liechtenstein) using liquid CO_2, mounted on aluminium stubs with double sided adhesive discs, coated with gold in a SCD 040 sputter coating unit (OC Oerlikon Balzers Coating, Balzers, Liechtenstein) and examined in a VEGA scanning electron microscope (TESCAN) operating at 5 kV.

The type specimens of the copepods collected in the present study were deposited in the Institute of Parasitology, Czech Academy of Sciences, České Budějovice, Czech Republic. Prevalence (percentage of infected fish) and mean intensity of infection (mean number of parasites per infected host) were calculated following Bush et al. (1997). Morphological terminology follows Huys and Boxshall (1991), and host nomenclature was checked against the World Register of Marine Species (WoRMS, www.marinespecies.org).

Molecular and phylogenetic analyses

Genomic DNA was extracted from each individual parasite specimen (or egg sacs only, when applicable) using DNeasy® Blood & Tissue Kit (Qiagen, Hilden, Germany) following the manufacturer's protocol. Three genetic markers were used for molecular identification of copepod species: two partial fragments of nuclear ribosomal DNA (rDNA) regions (28S and 18S rDNA) and one fragment of the mitochondrial cytochrome c oxidase subunit I (COI) gene. The primers used for amplification are listed in Table 2. PCR amplification and sequencing were conducted according to the protocols and conditions outlined in Míč et al. (2023), (2024)). Obtained sequences were edited using Sequencher® v.

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Table 3. List of Ergasilidae and Lernaeidae species molecularly analysed in this study, including their host species, locality, total number of isolates, GenBank accession numbers for 18S 28S, COI sequences and values of intraspecific genetic distances. For locality ID abbreviations see Table S2

					GB Acc. No.			Intraspecific p-distance		
Parasite species	Host species	Host family	Loc. ID	N. of isolates	18S	28S	COI	18S	28S	COI
Ergasilidae								Mean (in %)/number of genetic variants		
Ergasilus barbi	*Barbus escherichii*	Cichlidae	TUR8	3	PX000625	PX000652	–	0/1	0/1	NA
Ergasilus briani	*Alburnoides fasciatus*	Leuciscidae	TUR33	2	PX000629	PX000656	PV988327 (hap1)			
	Alburnus neretvae	Leuciscidae	BIH16	1	PX000626	PX000653	PV988324 (hap2)	0/1	0/1	0.81/3
	Gobio artvinicus	Gobionidae	TUR33	1	PX000630	PX000657	PV988328 (hap1)			
	Leucos aula	Leuciscidae	C1	1	PX000627	PX000654	PV988325 (hap2)			
	Leucos ylikiensis	Leuciscidae	G23	1	PX000628	PX000655	PV988326 (hap3)			
Ergasilus italicus n. sp.	*Protochondrostoma genei*	Leuciscidae	I4	2	PX000631	PX000658	–	0/1	0/1	NA
Ergasilus lizae	*Barbus sperchiensis*	Cyprinidae	G7	3	PX000632	PX000659	PV988329 (hap1), PV988330 (hap2)	0/1	0/1	0.47/3
	Luciobarbus graecus	Cyprinidae	G7	1	PX000633	PX000660	PV988331 (hap3)			
Ergasilus rostralis	*Barbus lacerta*	Cyprinidae	IRQ8	3	PX000634	PX000661	PV988332 (hap1), PV988333 (hap2), PV988334 (hap3)	0/1	0/1	0.21/3
Neoergasilus japonicus	*Chondrostoma regium*	Leuciscidae	IRQ11	1	PX000635 (v1)	PX000662 (v1)	PV988335 (hap1)	0.15/2	0.15/2	11.49/3
	Chondrostoma soetta	Leuciscidae	I8	1	PX000636 (v2)	PX000663 (v2)	PV988336 (hap2)			
	Leucos aula	Leuciscidae	C1	1	PX000637 (v1)	PX000664 (v1)	–			
	Squalius squalus	Leuciscidae	C8	1	PX000638 (v2)	PX000665 (v2)	PV988337 (hap3)			
Lernaeidae										
Lamproglena pulchella	*Barbus cyri*	Cyprinidae	TUR17	2	PX000643	PX000672 (v3)	PV988339 (hap2), PV988340 (hap3)			
	Garra rezai	Cyprinidae	TUR25	1	PX000644	PX000673 (v4)	PV988341 (hap4)			
	Gobio sakaryaensis	Gobionidae	TUR7	2	PX000645	PX000674 (v1)	–	0/1	0.37/4	13.82/4

(*Continued*)

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Table 3. (*Continued.*)

					GB Acc. No.			Intraspecific p-distance		
Parasite species	Host species	Host family	Loc. ID	N. of isolates	18S	28S	COI	18S	28S	COI
Ergasilidae								Mean (in %)/number of genetic variants		
	Protochondrostoma genei	Leuciscidae	I4	1	–	PX000667 (v1)	–			
	Scardinius plotizza	Leuciscidae	BIH15	1	PX000639	PX000666 (v1)	PV988338 (hap1)			
	Squalius fellowesii	Leuciscidae	TUR3	3	PX000642	PX000671 (v1)	–			
	Squalius orpheus	Leuciscidae	G5	1	PX000641	PX000670 (v2)	–			
	Squalius squalus	Leuciscidae	I3	1	PX000640	PX000668 (v1)	–			
	Squalius vardarensis	Leuciscidae	G3	1	–	PX000669 (v2)	–			
Lernaea cyprinacea	*Chondrostoma meandrense*	Leuciscidae	TUR53	1	PX000649	PX000678	–			
	Cyprinion kais	Cyprinidae	TUR26	1	PX000650	PX000679	PV988345 (hap2)	0/1	0/1	5.69/2
	Parachondrostoma arrigonis	Leuciscidae	S3	1	PX000648	PX000677	PV988344 (hap2)			
	Squalius tenellus	Leuciscidae	BIH6	1	PX000646	PX000675	PV988342 (hap1)			
	Squalius valentinus	Leuciscidae	S3	2	PX000647	PX000676	PV988343 (hap2)			
Pseudolamproglena zahrziensis n. sp.	*Carasobarbus luteus*	Cyprinidae	IRQ9, IRQ10, IRQ11	4	PX000651	PX000680	PV988346 (hap1), PV988347 (hap2), PV988348 (hap3), PV988349 (hap4)	0/1	0/1	0.27/3



Figure 2. Photomicrographs of representative species from the Mediterranean and the Middle East: (A) *E. barbi*; (B) antennae of *E. barbi*; (C) legs of *E. barbi*, spine on Exp-2 of L1 (white arrow); (D) *E. briani*; (E) antennae of *E. briani*; (F) urosome of *E. briani*, long caudal rami (white arrow); (G) *E. lizae*; (H) urosome of *E. lizae*; (I) antenna of *E. lizae*; (J) *E. rostralis*; (K) urosome of *E. rostralis*; (L) rostrum of *E. rostralis* (white arrow).

4.10.1 (Gene Codes Corporation, Ann Arbor, MI, USA), and the newly generated sequences for parasite species were checked by the nBLAST Search Tool (https://blast.ncbi.nlm.nih.gov/Blast.cgi) to assess any similarity to available congeners and deposited in GenBank (for accession numbers, see Table 3).

Molecular vouchers (hologenophores, paragenophores; Pleijel et al., 2008) were deposited in the Institute of Parasitology, Czech Academy of Sciences, České Budějovice, Czech Republic.

To investigate the phylogenetic position of collected parasitic copepods to the representatives of parasitic Cyclopoida, 59 sequences of 28S rDNA of the species belonging to 8 genera of Ergasilidae and 2 genera of Lernaeidae were retrieved from GenBank (for details, see Supplementary Table S3). The sequences were aligned with the G-INS-i method in MAFFT online service version 7 (Katoh et al., 2019) and ambiguous positions in the alignment were manually edited in BioEdit (Hall, 1999). ModelFinder (Kalyaanamoorthy et al., 2017) was employed to select the most appropriate model of DNA evolution. According to the Bayesian Information Criterion (BIC), GTR + F + I + G4 was selected as the best-fit model. Both maximum likelihood (ML) analysis and Bayesian inference (BI) were used to reconstruct the phylogenetic tree. The ML tree was constructed using an ultrafast bootstrap method (Hoang et al., 2018) with 1000 replicates in the IQ-TREE web server (Trifinopoulos et al., 2016). BI analysis was carried out in MrBayes 3.2.6 (Huelsenbeck and Ronquist, 2001), the analysis included 2 simultaneous runs of Markov chain Monte Carlo for 10^6 generations, sampling every 100 generations, with a 'burn-in' of 25%. The trees were visualized and

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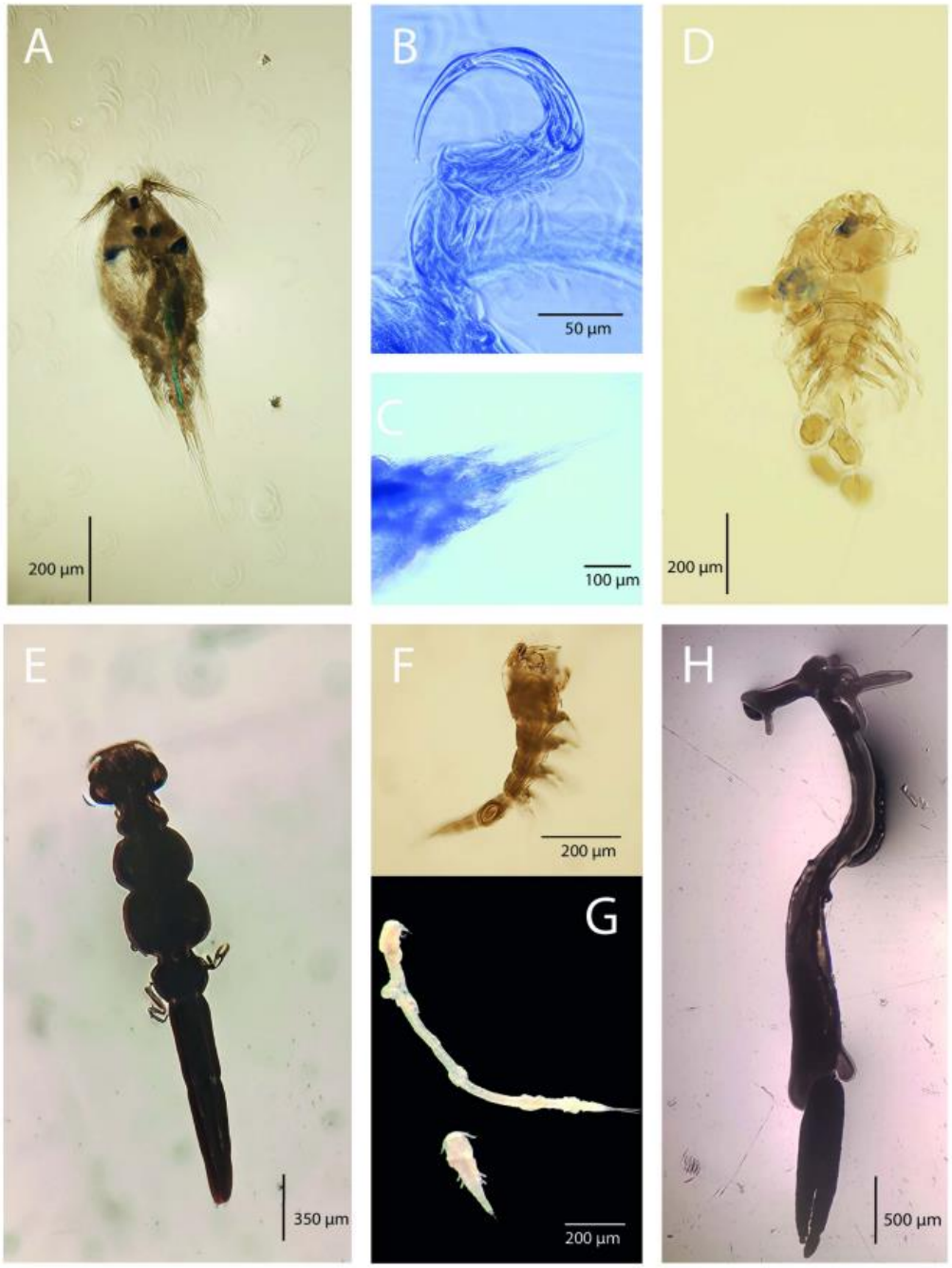


Figure 3. Photomicrographs of representative species from the Mediterranean and the Middle East: (A) *N. japonicus*; (B) antenna of *N. japonicus*; (C) urosome of *N. japonicus*; (D) *P. longidigitus*; (E) *L. pulchella*; (F) copepodid stage of *L. pulchella*; (G) copepodid stages of *L. cyprinacea*; (H) *L. cyprinacea*.

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edited in FigTree v. 1.4.3 (Rambaut, 2016) and Adobe Photoshop (Adobe Systems Inc., San Jose, CA, USA). Genetic distances (uncorrected *p*-distance) were calculated in MEGA v. 11 (Tamura et al., 2021).

Results

A total of 59 (39 Leuciscidae, 18 Cyprinidae and 2 Gobionidae; 35%) of the 169 fish species sampled in the Mediterranean and the Middle East watersheds were found to be positive for parasitic copepods of the Ergasilidae and Lernaeidae (1004 parasitic copepod adult females). The collected parasites were identified as 6 previously described species of Ergasilidae (*E. barbi, E. briani, E. lizae, E. rostralis, N. japonicus* and *P. longidigitus*) and 2 previously described species of Lernaeidae (*L. pulchella* and *L. cyprinacea*) based on their morphological and molecular characteristics (Figures 2 and 3). Additionally, two new species, *Ergasilus italicus* n. sp. found on *Protochondrostoma genei* (Bonaparte, 1839) in Italy and *Pseudolamproglena zahrziensis* n. sp. parasitizing *Carasobarbus luteus* (Heckel, 1843) in Iraq were described. Their morphological characterization and detailed description are provided below. All species are listed in Table 4, including their host(s), locality of collection, localization on fish and values of abundance, prevalence and intensity of infection. The full list of all fish examined (including non-infected fish) is given in Supplementary Tables S4 and S5.

Ergasilus briani was documented as the most abundant species, its occurrence was confirmed in Turkey, where it was previously recorded (Supplementary Table S1) and now we documented the presence of this species for the first time in Bosnia and Herzegovina, Croatia, Albania and Greece. *Ergasilus lizae* was found on two localities in Greece, confirming its previous presence. The occurrence of *E. barbi* in Turkey, *P. longidigitus* in Albania and *N. japonicus* in Croatia and Iraq were revealed for the first time. *Neoergasilus japonicus* was also found in Italy and Turkey, where its presence had been previously documented (Supplementary Table S1). Within Ergasilidae, the highest host range was observed for *N. japonicus* (14) and *E. briani* (10).

The occurrence of *L. pulchella* was confirmed in Italy and Turkey, and for the first time in Bosnia and Herzegovina and Greece. Moreover, this species exhibited the highest host range encompassing 19 host species (Table 4). *Lernea cyprinacea* was recorded on nine host species in Portugal, Spain, Croatia, Bosnia and Herzegovina and Turkey. It was the only copepod parasite recorded on the Iberian Peninsula in this study. All species of Lernaeidae were found in both copepodid and adult stages.

All *Ergasilus, Lamproglena* and *Pseudolamproglena* specimens were found on the gills, adult *Lernaea* specimens usually burrowed in the skin, *N. japonicus* was attached to the fins and *P. longidigitus* was found in the nasal cavity. Juvenile stages of *Lamproglena, Pseudolamproglena* and *Lernaea* were found on the gills. Each fish specimen typically harboured only a single species of parasitic copepod. Several cases of mixed infections, such as the co-infestation of gills by adult females of Ergasilidae and copepodid stages of Lernaeidae, were reported. The co-occurrence of *N. japonicus* on the fins and an ergasilid species on the gills of a single fish was also found.

Family Ergasilidae Burmeister, 1835

Genus *Ergasilus* Nordmann, 1832

Ergasilus italicus (Míč et al., 2024) n. sp.

Type-host: *Protochondrostoma genei* (Bonaparte, 1839) (Leuciscidae)

Type-locality: Torrente Cerfone, Tiber River drainage, Le Ville, Italy; 43°28′42′′N 12°04′25′′E

Type and voucher material: Holotype (adult female): IPCAS Cr-40 (1 specimen). Paratype (adult female): IPCAS Cr-40 (1 specimen). Hologenophores (adult females): IPCAS Cr-40 (2 specimens).

Site on host: Gill filaments.

Prevalence and intensity of infection: 44% (4 fish infected/9 fish examined); 1 specimen per infected host.

ZooBank registration: urn:lsid:zoobank.org:act:48903023-9FEB-4CD6-8F8B-2C0E10BF1EF7

Representative DNA sequences: A 1355 bp long 18S rDNA sequence and 640 bp long 28S rDNA sequence obtained from 2 specimens are deposited in the NCBI GenBank database under the accession numbers PX000631 and PX000658, respectively.

Etymology: The species was named after the country Italy where it was first discovered.

Description

Adult female. [Based on 4 specimens; Figures 4–7; measurements in Table 5]. Body length (measured from anterior margin of prosome to posterior margin of caudal rami) 1363 (1360-1365; $n = 4$). Body elongated and comprises prosome, urosome and caudal rami (Fig. 4A; 7A). Prosome 5-segmented, composed of cephalothorax and 3 free pedigerous somites; cephalosome and first pedigerous somite (PS-1) fused together, without distinct separation. Cephalothorax guitar-shaped, much longer than wide, bearing deep indentation between anterior cephalosome and posterior first pedigerous somite. Cephalic ornamentation comprising anterior circular eyespot and inverted T-shaped marking of thickened chitin situated medially on dorsal side. Paired sensory pores and papillae observed on the rostrum, anterior to eyespot and T-shaped marking, as well as on lateral margins of cephalosome (Figure 4E). Rostrum (Figure 4F) well-developed, with triangular posterior margin. Second to fourth pedigerous somites (PS-2 to PS-4) all wider than long and each markedly narrowing posteriorly.

Urosome (Fig. 5A; 7E) comprising fifth pedigerous somite (PS-5), genital double somite and 3 free abdominal somites (AS-1 to AS-3). PS-5 reduced but clearly visible, carrying rudimentary leg 5. Genital double-somite relatively small, wider than long, with transverse row of spinules and pair of hook-shaped ornamentation on ventral side, bearing pair of multiseriate egg sacs dorsally. Free abdominal somites decreasing in width posteriorly. AS-1 wider than long (2.8-3.1 times), slightly larger than AS-2 (1.2 times), bearing transverse row of spinules ventrally at widest part. AS-2 only slightly larger than AS-3 (1.07 times) with transverse row of spinules at midlength. AS-3 (= anal somite) deeply incised posteromedially, with spinules on posterior margin. Caudal rami slightly longer than AS-3 (1.07-1.1 times), slightly longer than wide (1.14-1.16 times) and ornamented with row of spinules towards distal margin. Each caudal rami ornamented ventrally with row of spinules on posterior margin and each bearing 3 terminal setae – innermost longest and thickest, ornamented with transversal rings of inconspicuous scales at posterior 3/4. Egg sacs (Figure 5B) long and multiseriate, much longer than wide (4.2 times), each composed of 2–3 rows of eggs.

Antennule (Figure 4D) 6-segmented, tapering, armed with long and short setae. The margin between the first and second segments inconspicuous (fused dorsally). Setal formula from proximal to distal segments: 3–13–5–3–2 + ae–6 + ae. Antenna (Fig. 4B; 7B)

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Table 4. List of collected parasitic copepods from respective hosts, including localities of their collection and their epidemiological statistics in the Mediterranean and the Middle East

Parasitic copepod	Host species	Host family	Loc. ID	N	NP	S	L	A	IN	P
Ergasilidae Burmeister, 1835										
Ergasilus barbi Rahemo, 1982	*Barbus escherichii**	Cyprinidae	TUR8	5	5	A	Gills	165	3–72	100%
	Barbus sp.*	Cyprinidae	TUR39	5	1	A	Gills	5	5	20%
	*Capoeta aydinensis**	Cyprinidae	TUR1	10	4	A	Gills	8	1–3	40%
	*Chondrostoma colchicum**	Leuciscidae	TUR6	5	1	A	Gills	1	1	20%
			TUR7	5	1	A	Gills	3	3	20%
Ergasilus briani Markevich, 1932	*Alburnoides fasciatus**	Leuciscidae	TUR33	5	3	A	Gills	14	2–9	60%
	*Alburnus neretvae**	Leuciscidae	BIH3	7	1	A	Gills	2	2	14%
			BIH16	10	9	A	Gills	52	1–14	90%
	*Alburnus scoranza**	Leuciscidae	A11	5	3	A	Gills	4	1	60%
	Alburnus sp.*	Leuciscidae	TUR37	10	1	A	Gills	1	1	10%
	*Gobio artvinicus**	Gobionidae	TUR33	5	1	A	Gills	41	41	20%
	*Leucos aula**	Leuciscidae	C1	10	5	A	Gills	16	1–5	50%
	*Leucos basak**	Leuciscidae	BIH1	13	12	A	Gills	205	5–27	92%
	*Leucos ylikiensis**	Leuciscidae	G23	9	8	A	Gills	84	1–25	89%
	*Squalius tenellus**	Leuciscidae	BIH5	3	1	A	Gills	1	1	33%
***Ergasilus italicus* n. sp.**	*Protochondrostoma genei**	Leuciscidae	I4	9	4	A	Gills	4	1	44%
Ergasilus lizae Krøyer, 1863	*Barbus cyclolepis**	Cyprinidae	G21	3	1	A	Gills	20	20	33%
	*Barbus sperchiensis**	Cyprinidae	G7	8	5	A	Gills	87	1–64	63%
	*Luciobarbus graecus**	Cyprinidae	G7	3	3	A	Gills	5	1–2	100%
Ergasilus rostralis Ho et al., 1992	*Barbus lacerta**	Cyprinidae	IRQ8	10	3	A	Gills	7	1–4	30%
	*Capoeta umbla**	Cyprinidae	IRQ7	10	1	A	Gills	1	1	10%

(*Continued*)

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Table 4. (*Continued.*)

Parasitic copepod	Host species	Host family	Loc. ID	N	NP	S	L	A	IN	P
Neoergasilus japonicus (Harada, 1930)	*Acanthobrama marmid**	Leuciscidae	IRQ11	10	1	A	Fins	1	1	10%
	*Alburnus arborella**	Leuciscidae	I1	10	1	A	Fins	1	1	10%
	*Alburnus sellal**	Leuciscidae	IRQ1	2	1	A	Fins	2	1	50%
			IRQ2	1	1	A	Fins	1	1	100%
			IRQ9	7	1	A	Fins	1	1	14%
	*Carasobarbus luteus**	Cyprinidae	IRQ3	3	1	A	Fins	1	1	33%
	*Chondrostoma soetta**	Leuciscidae	I8	5	2	A	Fins	2	1	40%
	*Chondrostoma regium**	Leuciscidae	IRQ11	6	6	A	Fins	18	1 – 5	100%
	*Chondrostoma turnai**	Leuciscidae	TUR4	5	3	A	Fins	22	1 – 18	60%
	*Cyprinion macrostomus**	Cyprinidae	IRQ1	5	2	A	Fins	2	1	40%
			IRQ3	9	3	A	Fins	3	3	33%
	*Leucos aula**	Leuciscidae	C1	10	2	A	Fins	3	1 – 2	20%
	*Luciobarbus schejch**	Cyprinidae	IRQ11	7	2	A	Fins	2	1	29%
	*Scardinius dergle**	Leuciscidae	C1	10	1	A	Fins	1	1	10%
	*Squalius lepidus**	Leuciscidae	IRQ11	9	4	A	Fins	7	1 – 3	44%
	*Squalius squalus**	Leuciscidae	C8	10	3	A	Fins	4	2	30%
	*Vimba mirabilis**	Leuciscidae	TUR4	10	3	A	Fins	5	1 – 3	30%
Paraergasilus longidigitus Yin, 1954	*Alburnoides fangfangae**	Leuciscidae	A7	7	1	A	Nose	1	1	14%
	*Alburnus scoranza**	Leuciscidae	A11	5	2	A	Nose	2	1	40%
Lernaeidae Cobbold, 1879										
Lamproglena pulchella von Nordmann, 1832	*Acanthobrama microlepis**	Leuciscidae	TUR18	5	1	A	Gills	1	1	20%
	*Alburnoides ohridanus**	Leuciscidae	G27	10	1	A	Gills	1	1	10%
	*Barbus cyri**	Cyprinidae	TUR17	4	2	A	Gills	5	2 – 3	50%

(*Continued*)

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Table 4. (*Continued.*)

Parasitic copepod	Host species	Host family	Loc. ID	N	NP	S	L	A	IN	P
	*Capoeta capoeta**	Cyprinidae	TUR15	7	1	A	Gills	1	1	14%
	*Capoeta sieboldii**	Cyprinidae	TUR6	7	1	A	Gills	1	1	14%
	*Capoeta tinca**	Cyprinidae	TUR6	5	1	A	Gills	4	4	20%
	*Garra rezai**	Cyprinidae	TUR25	5	3	A	Gills	3	1	60%
	*Gobio sakaryaensis**	Gobionidae	TUR7	10	4	A	Gills	22	1 – 12	40%
	*Protochondrostoma genei**	Leuciscidae	I4	9	2	A	Gills	4	1 – 3	22%
	*Sarmarutilus rubilio**	Leuciscidae	I3	10	1	A	Gills	1	1	10%
	*Scardinius acarnanicus**	Leuciscidae	G19	4	2	A	Gills	5	2 – 3	50%
	*Scardinius plotizza**	Leuciscidae	BIH15	7	6	A	Gills	20	1 – 6	86%
	*Squalius fellowesii**	Leuciscidae	TUR3	10	10	A	Gills	58	1 – 13	100%
	*Squalius orpheus**	Leuciscidae	G5	1	1	A	Gills	4	4	100%
	*Squalius pamvoticus**	Leuciscidae	G16	6	1	A	Gills	1	1	17%
	*Squalius prespensis**	Leuciscidae	G20	6	1	A	Gills	1	1	17%
			G27	1	1	A	Gills	3	3	100%
	*Squalius squalus**	Leuciscidae	I3	11	1	A	Gills	4	4	9%
	*Squalius vardarensis**	Leuciscidae	G3	7	1	A	Gills	1	1	14%
	*Telestes pleurobipunctatus**	Leuciscidae	G17	6	3	A	Gills	3	1 – 2	50%
	Telestes sp.*	Leuciscidae	G26	11	2	A	Gills	2	1	18%
Lernaea cyprinacea Linnaeus, 1758	*Capoeta damascina*	Cyprinidae	TUR21	4	1	A	Skin	1	1	25%
	*Chondrostoma meandrense**	Leuciscidae	TUR53	9	1	A	Skin	1	1	11%
	*Cyprinion kais**	Cyprinidae	TUR26	8	1	A	Skin	2	2	13%
	Leucos aula	Leuciscidae	C1	10	1	A	Skin	1	1	10%
	*Luciobarbus guiraonis**	Cyprinidae	S2	1	1	A	Skin	13	13	100%
			S3	10	3	A	Skin	3	1	30%
			S4	1	1	A	Skin	2	2	100%

(*Continued*)

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Table 4. (*Continued.*)

Parasitic copepod	Host species	Host family	Loc. ID	N	NP	S	L	A	IN	P
	*Parachondrostoma arrigonis**	Leuciscidae	S3	3	1	A	Skin	1	1	33%
	Pseudochondrostoma polylepis	Leuciscidae	P4	15	1	A	Skin	1	1	7%
	*Squalius pyrenaicus**	Leuciscidae	S7	5	1	A	Skin	1	1	20%
	*Squalius tenellus**	Leuciscidae	BIH6	11	1	A	Skin	2	2	9%
	*Squalius torgalensis**	Leuciscidae	P6	10	3	A	Skin	3	1	30%
	*Squalius valentinus**	Leuciscidae	S3	5	5	A	Skin	7	1–3	100%
***Pseudolamproglena zahrziensis* n. sp.**	*Carasobarbus luteus**	Cyprinidae	IRQ9	8	5	A	Gills	6	1–4	63%
			IRQ10	2	2	A	Gills	7	7	50%
			IRQ11	3	2	A	Gills	3	1–2	67%

Notes: N – number of fish hosts; NP – number of fish hosts positive for parasitic copepods; S – stage; L – localization on the host; A – abundance; IN – intensity of infection (min – max); P – prevalence; * – new host records for the species

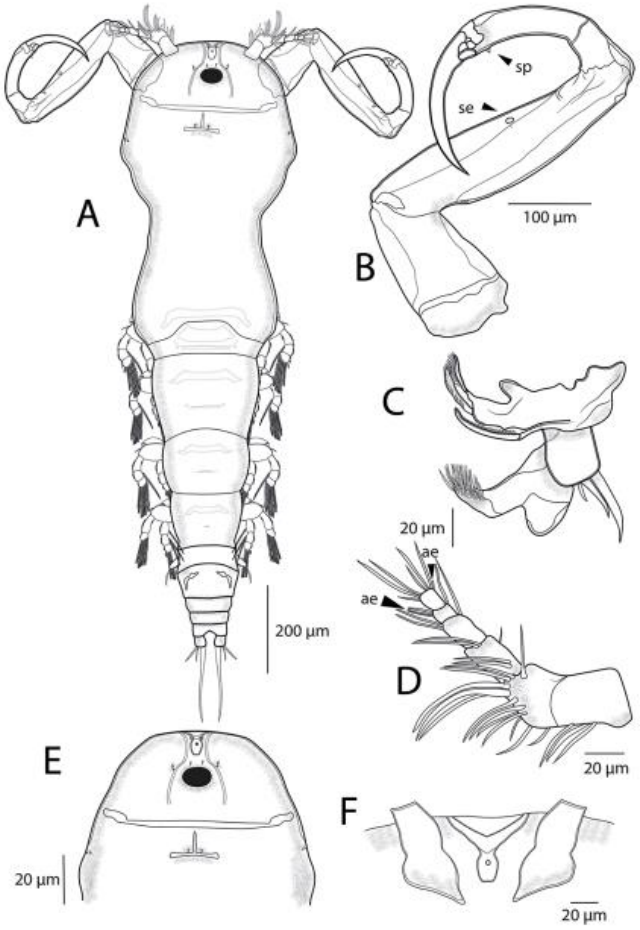


Figure 4. *Ergasilus italicus* Mič & Seifertová, 2025 n. sp., paratype female. (A) habitus, dorsal; (B) antenna with spine (sp) and sensillum (se), ventral; (C) mouthparts, ventral; (D) antennule, distal segment 2 aesthetasc (ae), ventral; (E) cephalosome, dorsal; (F) rostrum, ventral.

4-segmented, comprising coxobasis, 3-segmented endopod (Enp-1 to Enp-3) and curved terminal claw. Enp-1 (proximal) longest, nearly 1.55 times longer than coxobasis, tapering distally, bearing one sensillum distally on the concave margin; Enp-2 (medial) elongated, slightly curved, about 0.7 length of Enp-1, with prominent spine distally on anterior margin and with conspicuous groove in cuticle on inner side (Figure 7C, F). Enp-3 inconspicuous, unornamented. Terminal claw long and curved, about 0.7 size of Enp-2, unornamented.

Mouthparts (Fig. 4C; 7H) comprising mandible, maxillule and maxilla; maxilliped absent. Mandible consisting of 3 blades (anterior, middle and posterior); anterior blade with sharp teeth on anterior margin; middle blade with sharp teeth on both margins; and posterior blade with sharp teeth on anterior margin. Maxillule bearing 2 unequally long smooth outer setae and 1 minute inner seta. Maxilla 2-segmented, comprising unarmed syncoxa and basis, distally with numerous sharp teeth on anterior margin.

Swimming legs (L1 to L4) biramous; each comprising coxa, basis, endopod (inner ramus) and exopod (outer ramus) (Figure 6). Intercoxal sclerites (Figure 5D) slender; each with tapering ends directed posterolaterally, unornamented. Interpodal plates slender (Figure 5D), each different in shape and decreasing in size, each with 2 inconspicuous bilateral pores and row of spinules. Armature formula of L1–L4 (spines – Roman numerals; setae – Arabic numerals) shown in Table 6.

Coxa of all legs unarmed; coxa of L1-L4 with a row of spinules extending along its outer posterior margin. Basis of all legs armed with proximal outer spine, unornamented. L1–L4 with outer margin of both rami ornamented with rows of spinules; outer and inner margin of first endopodal and exopodal segment, respectively, of all legs partly or completely covered with bristles.

Leg 1 (Fig. 6A; 7E): exopod 3-segmented; first segment with small naked spine arising from outer posterior margin; second segment with small naked spine arising from outer posterior margin

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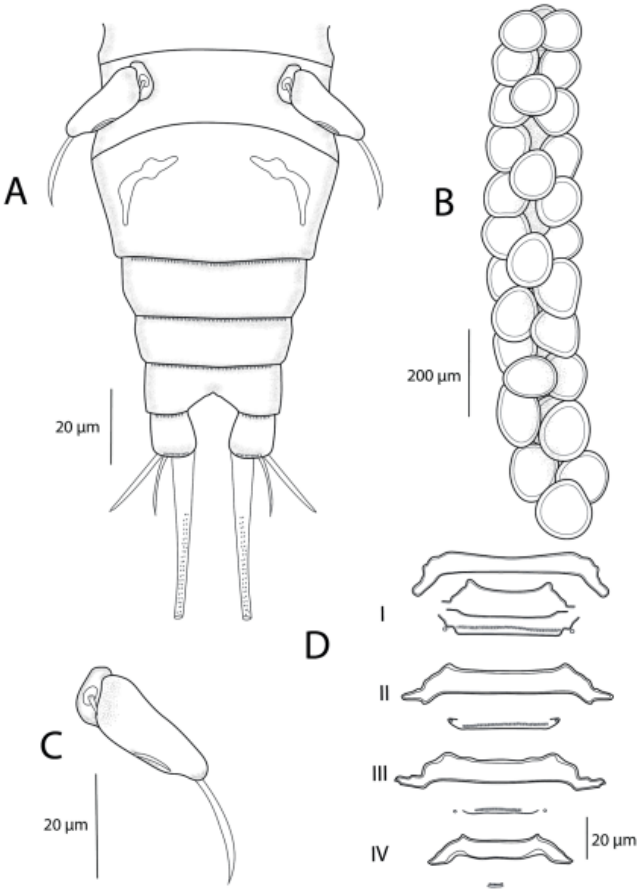


Figure 5. *Ergasilus italicus* Mič & Seifertová, 2025 n. sp., paratype female. (A) abdomen and caudal rami; (B) egg sac, dorsal; (C) leg 5, ventral; (D) interpodal plates, ventral.

and 1 inner plumose seta; third segment with 2 blade-like serrated spines (shorter more proximal) and 5 plumose setae. Endopod 3-segmented; first and second segments each with 1 plumose seta; third segment with 4 plumose setae and 2 blade-like serrated spines.

Leg 2 (Fig. 6B; 7D): exopod 3-segmented; first segment with small naked spine arising from outer posterior margin; second segment with 1 plumose seta; third segment with 6 plumose setae. Endopod 3-segmented; first and second segments each with 1 plumose seta; third segment with 1 blade-like serrated spine and 4 plumose setae.

Leg 3 (Figure 6C) with same ornamentation and armament described for L2.

Leg 4 (Figure 6D): exopod 2-segmented; first segment elongated, with small naked spine arising from outer posterior margin; second segment with 5 plumose setae. Endopod 3-segmented; first segment with 1 plumose seta; second segment with 2 plumose setae; third segment with 1 slender blade-like serrated spine and 3 plumose setae.

Leg 5 (Fig. 5C; 7G): reduced, but clearly visible, 2-segmented. Basal segment very small, bearing outer seta. Distal segment rectangular with 1 small seta on lateral margin and 1 long apical seta.

Specimens preserved in ethanol faint brown in colour, with dark brown spots in the cephalothorax.

Male: unknown

Remarks

Ergasilus italicus n. sp. has a combination of unique morphological characteristics distinguishing it from other species of *Ergasilus*. The most prominent distinguishing features are the morphology of the cephalothorax, and the leg armature formula. With an overall mean body length exceeding 1350 µm, *E.italicus* n. sp. also belongs to one of the largest species currently known.

The leg armature formula of *E. italicus* n. sp. closely resembles that of *E. sieboldi*, particularly in the presence of a spine on the outer margin of the second exopod segment of leg 1. However, a

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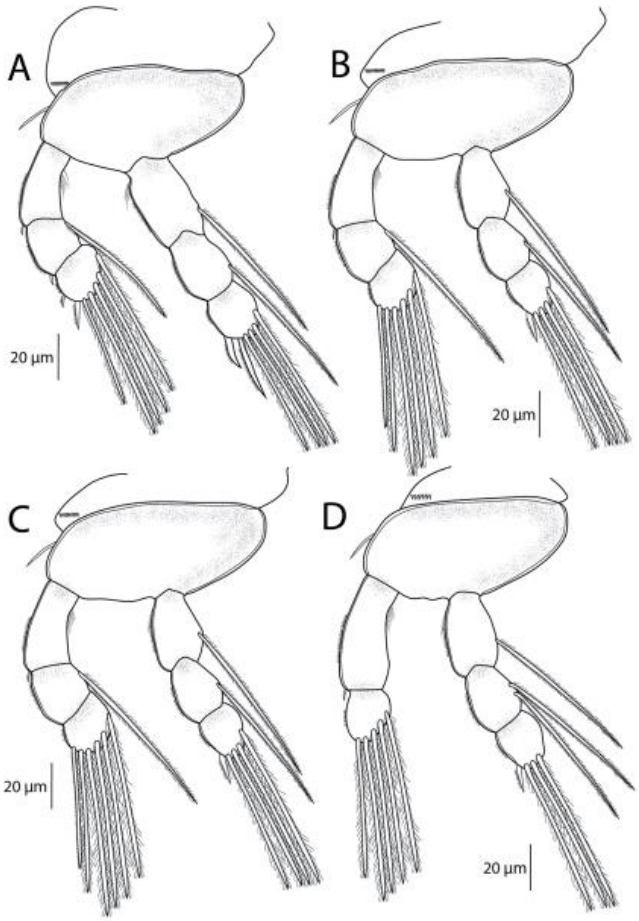


Figure 6. *Ergasilus italicus* Mič & Seifertová, 2025 n. sp., paratype female. (A) leg 1, ventral; (B) leg 2, ventral; (C) leg 3, ventral; (D) leg 4, ventral.

key difference lies in the armature of the second endopod segment of legs 2 and 3. While most species of *Ergasilus* carry 2 inner setae on this segment, *E. italicus* n. sp. bears only 1 seta. This feature is shared among European species only with *E. gibbus* and *Ergasilus tumidus* Markevich, 1940, but *E. italicus* n. sp. differs from *E. gibbus* by having: (i) two-segmented leg 5 (*vs* small one-segmented papilla); (ii) 2 setae on the second endopod segment of leg 4 (*vs* 1 seta); (iii) 2 unequal setae and 1 minute seta on maxillule (*vs* only 2 setae on maxillule); and from *E. tumidus* by having: (i) spine on Enp-2 of the antenna (*vs* absence); (ii) two-segmented leg 5 (*vs* small one-segmented papilla); (iii) outer spine on Enp-3 of legs 2 and 3 (*vs* absence). All other species of *Ergasilus* recorded in Europe are characterized by the presence of 2 setae on the second endopod segment of legs 2 and 3. The descriptions of *Ergasilus boettgeri* Reichenbach-Klinke, 1958, *Ergasilus osmeri* Beneden, 1870 and *Ergasilus suboculatus* (Hesse, 1871) do not include the leg armature formula. However, based on the available drawings, the shape of the cephalothorax and antenna do not match *E. italicus* n. sp.

The guitar-shaped cephalothorax has been noted in 12 currently known species worldwide: *Ergasilus arthrosis* (Roberts, 1970) from the USA; *Ergasilus atafonensis* Amado & Rocha, 1996 from Brazil; *Ergasilus bahiensis* Amado & Rocha, 1996 from Brazil; *E. barbi* from Iraq; *E. briani* from many countries in Europe and China; *Ergasilus curticrus* Muriel-Hoyos, Santana-Pineros, Cruz-Quintana & Suarez-Morales, 2015 from Colombia; *Ergasilus cyanopictus* Carvalho, 1962 from Brazil; *E. iraquensis* from Iraq; *Ergasilus mirabilis* Oldewadge & Van As, 1987 from South Africa; *E. mosulensis* from Iraq and *Ergasilus parabahiensis* El-Rashidy & Boxshall, 1999 from Guyana.

Only 3 species (*E. barbi, E. luteusi* and *E. mosulensis*) share the combination of the guitar-shaped cephalothorax and in the same time have only 1 seta on the armature of the second endopod segment of legs 2 and 3. The new species differs from *E. barbi* by having: (i) only 1 spine on the antenna (*vs* 3 spines on the antenna); (ii) only 2 setae on leg 5 (*vs* 3 setae on leg 5); (iii) mean body length over 1350 µm (*vs* mean body length

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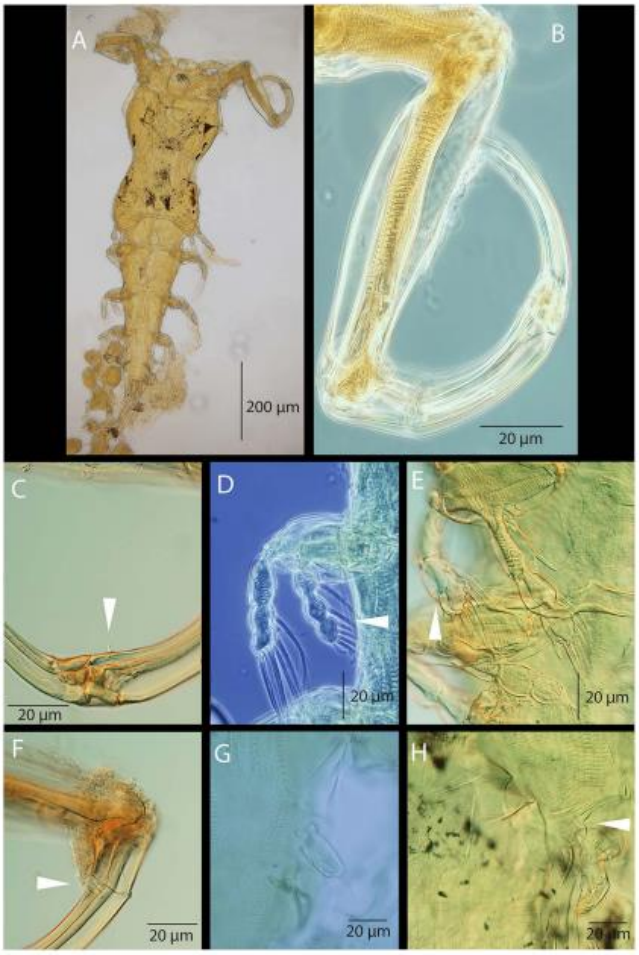


Figure 7. Light microscope photographs of *Ergasilus italicus* Mič & Seifertová, 2025 n. sp., paratype female. (A) habitus, dorsal; (B) antenna, ventral; (C) spine on the antenna (arrow); (D) leg 2 with only 1 seta on the second segment of endopod (arrow); (E) leg 1 with spine on the second segment of exopod (arrow), dorsal; (F) groove on the antenna (arrow); (G) leg 5; (H) maxillule with 3 setae (arrow)

813–1138 µm). It is clearly distinguished from *E. luteusi* by having: (i) cephalosome completely fused with the first pedigerous somite (*vs* well-developed depression between the cephalosome and the first pedigerous somite; (ii) only 1 spine on the antenna (*vs* 3 spines on the antenna); (iii) 2 unequal setae and 1 minute seta on maxillule (*vs* only 2 unequal setae on maxillule). It also differs from *E. mosulensis* by having: (i) an outer spine on the second segment of the exopod of leg 1 (*vs* absence); (ii) only 1 spine on the antenna (*vs* 3 spines on the antenna); (iii) only 2 setae on leg 5 (*vs* 3 setae on leg 5).

E. italicus n. sp. represents the second ergasilid copepod described solely from Italy (after *Ergasilus lagunaris* Grandori, 1925).

Family Lernaeidae Cobbold, 1879

Genus *Pseudolamproglena* (Boxshall, 1976)

Pseudolamproglena zahrziensis (Míč et al., 2024) n. sp.

Type-host: *Carasobarbus luteus* (Heckel, 1843) (Cyprinidae)

Type-locality: Zahrzi, Tabin River, Tigris River drainage, Iraq; 35°48′32″N 45°01′20″E

Additional localities: Grdi Go, Zalm Stream, Tigris River drainage, Iraq; 35°18′26″N 45°58′18″E and Du Choman, Aw-e Shiler River, Tigris River drainage, Iraq; 35°45′49″N 45°27′12″E

Type and voucher material: Holotype (adult female): IPCAS Cr-41 (1 specimen). Paratypes (adult females): IPCAS Cr-41 (1 specimen). Hologenophores (adult females): IPCAS Cr-41 (3 specimens).

Site on host: Gill filaments.

Prevalence and intensity of infection: 69% (9 fish infected/13 fish examined); 1–4 specimens per infected host.

ZooBank registration: urn:lsid:zoobank.org:act:00366F43-B1C2-4F48-9040-5B8B3FE43BA7

Representative DNA sequences: A 1395 bp long 18S rDNA sequence, 733 bp long 28S rDNA sequence and 3 haplotypes of 620 bp long COI sequences obtained from 4 specimens are deposited

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Table 5. Measurements (in micrometres) of specimens ($n = 4$) of *Ergasilus italicus* n. sp. parasitizing *Protochondrostoma genei* in Italy

Character	Range	Mean
Total length	1360–1365	1363
Body width	400–403	401
Cephalosome length	Fused	NA
Cephalosome width	399–402	400
Antennule length	128–132	129
Antenna length	674–699	680
Antennal segment 1 length	154–156	155
Antennal segment 2 length	232–250	240
Antennal segment 3 length	165–170	168
Antennal segment 4 (claw) length	123–125	124
Cephalothorax length	616–625	622
Cephalothorax width	342–345	344
Pedigerous somite 2 length	161–169	164
Pedigerous somite 2 width	238–247	242
Pedigerous somite 3 length	154–158	155
Pedigerous somite 3 width	183–194	187
Pedigerous somite 4 length	109–119	115
Pedigerous somite 4 width	134–141	136
Pedigerous somite 5 length	39–40	39
Pedigerous somite 5 width	109–114	112
Genital double somite length	81–83	82
Genital double somite width	110–114	112
Abdominal somite 1 length	28–29	29
Abdominal somite 1 width	96–98	97
Abdominal somite 2 length	25–26	25
Abdominal somite 2 width	77–79	78
Abdominal somite 3 length	21–23	22
Abdominal somite 3 width	66–67	66
Caudal ramus length	23–25	24
Caudal ramus width	20–23	21
Egg-sac length	562–575	565
Egg-sac width	134–137	135

Table 6. Spine (Roman numerals) and setal (Arabic numerals) formula of swimming legs of Ergasilus italicus n. sp

	Coxa	Basis	Exopod	Endopod
Leg 1	0–0	1–0	I–0; I–1; II–5	0–1; 0–1; II–4
Leg 2	0–0	1–0	I–0; 0–1; 0–6	0–1; 0–1; I–4
Leg 3	0–0	1–0	I–0; 0–1; 0–6	0–1; 0–1; I–4
Leg 4	0–0	1–0	I–0; 0–5	0–1; 0–2; I–3

in the NCBI GenBank database under the accession numbers PX000651, PX000680 and PV988346–PV988349, respectively.

Etymology: The species was named after the city of Zahrzi in Iraq, near which it was first discovered.

Description

Adult female. [Based on 10 specimens; Figures 8–10].

Body length (measured from anterior margin of head to posterior margin of caudal rami) 2172 µm (1816–2445 µm; $n = 10$). Body cylindrical and indistinctly segmented (Fig. 8A, B; 10A). Cephalothorax (Fig. 8C; 10B) broad, dorsal surface concave, comprising 16-20% of total body length. First pedigerous somite incorporated into cephalothorax, narrowing posteriorly to form 'neck' between cephalothorax and trunk. Second to fourth pedigerous somites separated by intersegmental sutures, subdivided into anterior and posterior portions by a transverse groove, equal in width. Thoracic legs located anterior to groove. Pedigerous somites increasing in size posteriorly.

Genital complex small, narrower than fourth pedigerous somite and with conspicuous dorsal swellings marking the genital apertures situated dorso-laterally. Abdomen elongate (Figure 10D), consisting of two indistinctly divided somites, narrower than fourth pedigerous somite and genital complex. Posterior margin of anal somite bilobate, bearing medially directed caudal rami. Egg string (Figure 9F) uniseriate, containing up to 21 eggs.

Antennule (Figure 8E) situated on ventral surface near anterior margin of cephalothorax, directed posterolaterally, only apical segment clearly delimited. Armature comprising 8 setae on anterior margin of proximal segment, 3 setae on distal segment and 2 aesthetasc-like structures.

Antenna (Figure 8F) situated lateral to transverse ridge on ventral surface of cephalothorax, curved posteriorly, indistinctly two-segmented with 3 longer and 1 shorter setae.

Oral region (Fig. 8C; 10B) occupied by large trilobed labrum. Transverse ridge present on ventral surface of cephalothorax anterior to trilobed labrum. Maxillule absent. Maxilla (Fig. 8G; 10C) large, indistinctly two-segmented; proximal segment broad, distal segment marked by transverse constriction and armed with robust dorsally curved claw on medial surface. Maxilliped (Figure 8H) indistinctly three-segmented, proximal segment connected by transverse ridge of tissue on ventral surface, middle segment elongated and widening distally, terminal segment round and armed with two setiform spines on medial surface.

Thoracic legs 1-4 (Figure 9) similar, biramous. Sympod projecting from body surface, bearing single seta lateral to exopod base. Endopod indisctinctly two-segmented, exopod three-segmented. Leg 1 (Fig. 9A; 10E) sympod with serrated distal margin; endopod with one terminal seta; exopod with 3 terminal setae and 1 lateral spine on both middle and proximal segments. Leg 2 (Fig. 9B; 10E) endopod unarmed; exopod with 3 short terminal setae on distal segment. Leg 3 (Figure 9C) endopod unarmed; exopod with 3 short terminal setae on distal segment and 1 lateral spine on proximal segment. Leg 4 (Figure 9D) endopod unarmed; exopod with 3 terminal setae on distal segment and 1 lateral spine on both middle and proximal segments. Leg 5 (Fig. 9E; 10F) simple process with 2 apical setae, positioned anteriorly on ventral surface of genital complex.

Caudal ramus (Figure 8D) armed with 3 setae; 1 on lateral margin and 2 at each posterolateral corner. Two small papillae present on distal margin.

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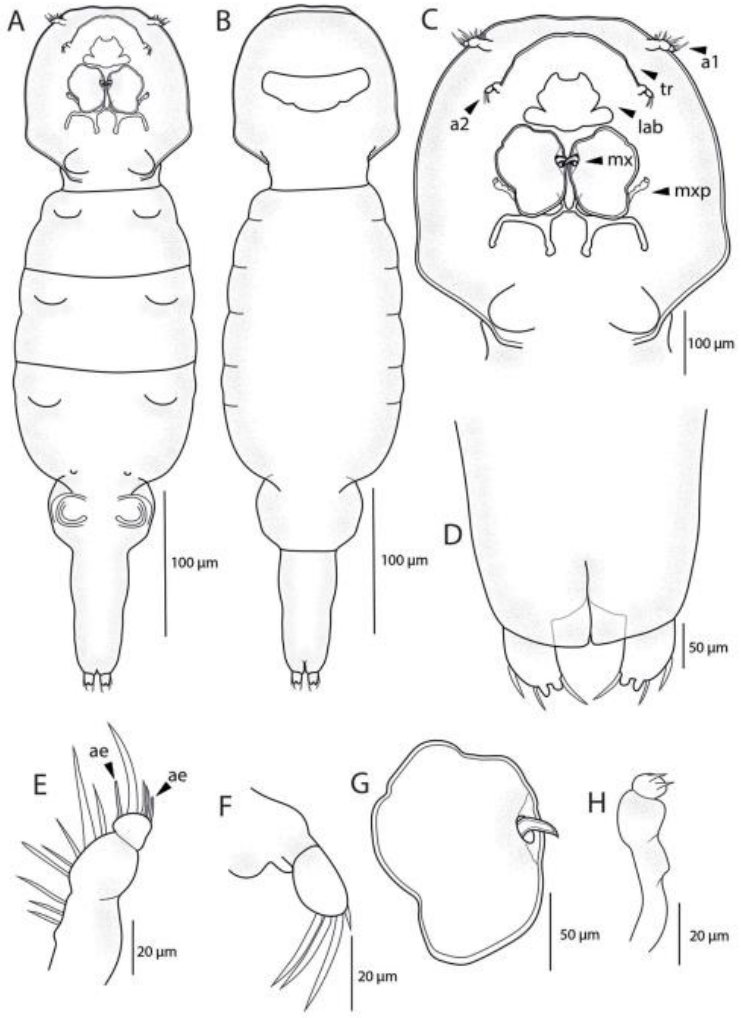


Figure 8. *Pseudolamproglena zahrziensis* Mič & Seifertová, 2025 n. sp., paratype female. (A) habitus, ventral; (B) habitus, dorsal; (C) cephalothorax with antennule (a1), antenna (a2), transversal ridge (tr), labrum (lab), maxilla (mx), maxilliped (mxp), ventral; (D) caudal rami; (E) antennule, distal segment 2 aesthetasc (ae); (F) antenna; (G) maxilla; (H) maxilliped.

Remarks

Currently, there are 4 species of *Pseudolamproglena* described, with similar general body shape, but differences in other morphological traits. *Pseudolamproglena sinilabis* (Kuang, 1980) is the longest of all the species of the genus, with the total length of 2930–3670 µm (Kuang, 1980). In comparison, *P. boxshalli* is less than 2600 µm, *Pseudolamproglena simplex* (Boxshall, 1976) less than 2450 µm (Boxshall, 1976) and *P. annulata* less than 2200 µm (Boxshall, 1976), while the newly described species less than 2450 µm. *P. zahrziensis* n. sp. is also distinguishable from *P. sinilabis* in its armature on the antenna with 4 setae (*vs* 8), bearing three-segmented exopods on all four pairs of legs (*vs* two-segmented exopods), caudal rami with 3 setae (*vs* 6) and posession of maxillipeds (*vs* maxillipeds absent).

P. zahrziensis n. sp. shares the same armature of the maxillipeds (2 setae on the distal segment) with *P. simplex*, but differs from it by having more distinctly segmented body, the absence of maxillules (*vs* presence), a presence of trilobed labrum in the oral region (*vs* hemispheric labrum), caudal rami with 3 setae (*vs* 6) and differences in the armature of the legs 1-4.

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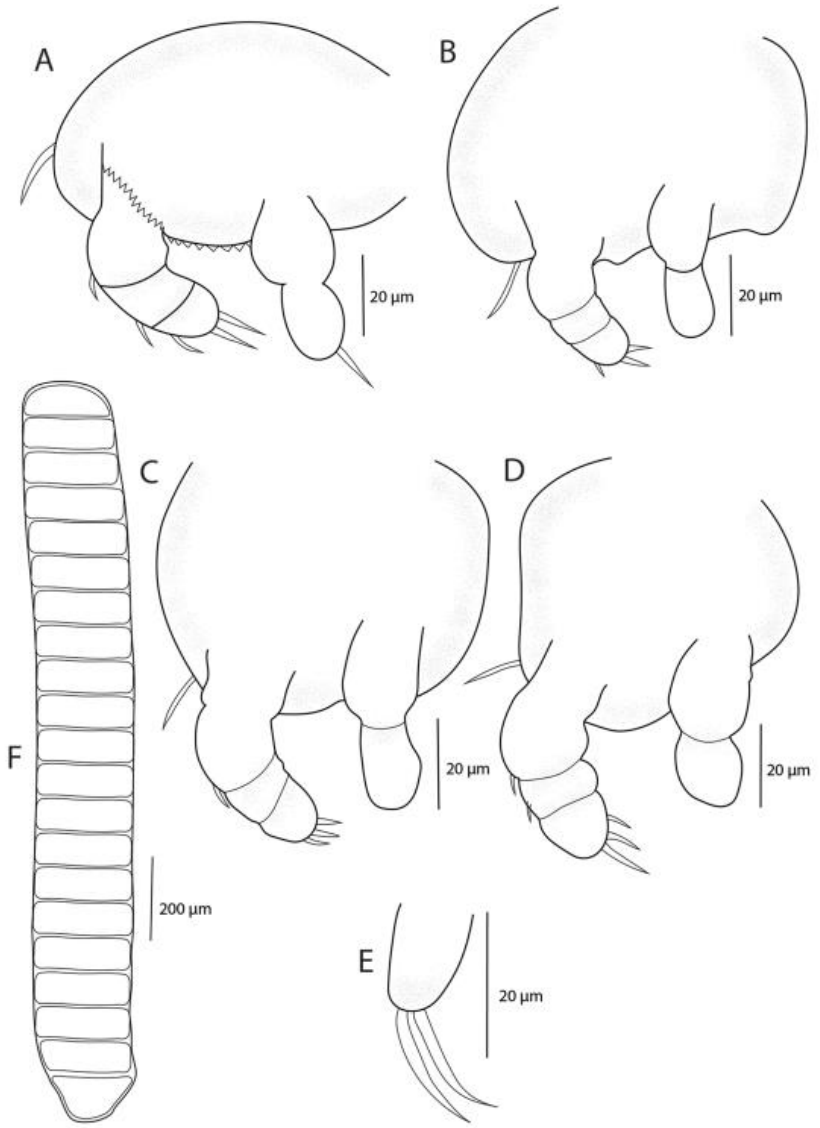


Figure 9. *Pseudolamproglena zahrziensis* Mič & Seifertová, 2025 n. sp., paratype female. (A) leg 1; (B) leg 2; (C) leg 3; (D) leg 4; (E) leg 5; (F) egg sac.

P. zahrziensis n. sp. is similar to *P. annulata* and *P. boxshalli* in its distinctly segmented body, the absence of the maxillule and the presence of the large trilobate labrum in the oral region. It also shares the same caudal rami armature (3 setae) and serrated distal margin of sympod with *P. boxshalli*, and similar antennule armature (8 setae on the proximal segment) and presence of single seta lateral to exopod of legs 1-4 with *P. annulata*. However, it differs from *P. annulata* in the armature of the maxillipeds with 2 setae on the distal segment (*vs* 1), caudal rami with 3 setae (*vs* 4), serrated distal margin of sympod (*vs* smooth) and differences in the armature of the legs 1-4. From *P. boxshalli* it differs in the armature of the maxillipeds with 2 setae on the distal segment (*vs* 9), the armature of the antennules with 8 setae on the proximal segment (*vs* 14), presence of single seta lateral to exopod of

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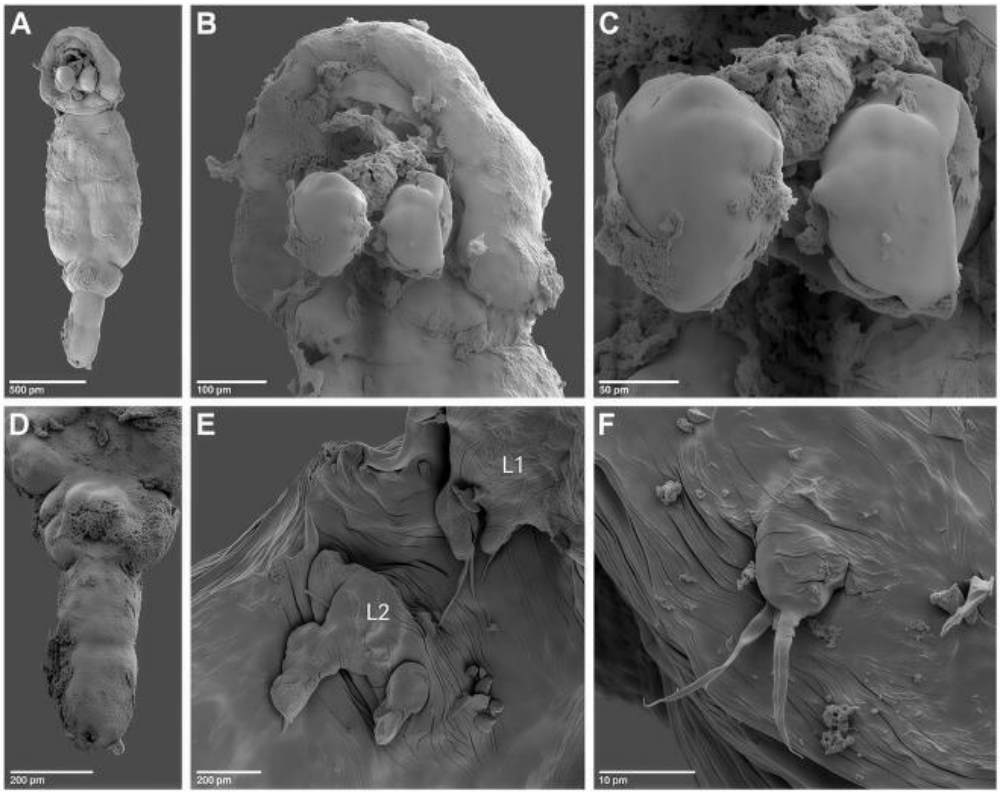


Figure 10. Scanning electron micrographs of *Pseudolamproglena zahrziensis* Míč & Seifertová, 2025 n. sp., paratype female. (A) habitus, ventral; (B) cephalothorax, ventral; (C) maxilla; (D) abdomen and caudal rami, ventral; (E) leg 1 and leg 2; (F) leg 5.

legs 1-4 (*vs* absence) and in differences in the armature of the legs 1-4.

Molecular characterisation and phylogenetic relationships of Mediterranean and Middle East Ergasilidae and Lernaeidae

In this study, the first molecular data were obtained for parasite copepod species *E. barbi, E. lizae, E. rostralis* and *L. pulchella*. Despite many attempts, no molecular data were obtained for specimens of *P. longidigitus*, probably due to inappropriate fixation or drying up of the specimens during long term storage. No intraspecific genetic variability was observed for rDNA sequences of *E. barbi, E. briani, E. lizae, E. italicus* n. sp., *P. zahrziensis* n. sp. and *L. cyprinacea*. Two genetic variants of 18S and 28S rDNA were observed for *N. japonicus* (variant 1: PX000635, PX000637 (18S), PX000662, PX000664 (28S); variant 2: PX000636, PX000638 (18S), PX000663, PX000665 (28S)), which were identical with 2 type of genetic variants previously observed in the Czech Republic (Ondračková et al., 2019). For *L. pulchella*, 4 closely related genetic variants of 28S rDNA (variant 1: PX000666, PX000667, PX000668, PX000671, PX000674; variant 2: PX000669, PX000670; variant 3: PX000672; variant 4: PX000673), but only one variant of 18S rDNA were found. Intraspecific mean *p*-distance values are listed in Table 3. From 2 to 4 unique COI haplotypes were obtained for species studied, except *E. italicus* n. sp. and *E. barbi* (even if several PCR modifications and primers combinations were tested, PCR failed). The intraspecific COI variation ranged from 0.21 % in *E. rostralis* to 13.82 % in *L. pulchella* (Table 3).

The tree topologies obtained by ML and BI methods were almost identical, and the resulting phylogram based on the ML analysis of 28S rDNA sequences with posterior probabilities (BI) and bootstrap values (ML) along nodes is presented in Figure 11. The phylogenetic analyses confirmed the presence of several well-supported clades congruent with previous studies (e.g. Míč et al., 2023, 2024; Jansen et al., 2024; Narciso et al., 2024). The species of the Ergasilidae formed 6 well-supported clades (A-F, Figure 11). Species of *E. barbi, E. lizae, E. rostralis* and *E. italicus* n. sp. were placed in clade A (BI = 0.98; ML = 97), which includes species parasitizing African cichlids [*Ergasilus macrodactylus* (Sars, 1909), *Ergasilus parvus* (Míč et al., 2023), *Ergasilus kandti* van Douwe, 1912, *Ergasilus megacheir* (Sars, 1909), *Ergasilus parasarsi* (Míč et al., 2023) and *Ergasilus caparti* (Míč et al., 2023)] and catfishes

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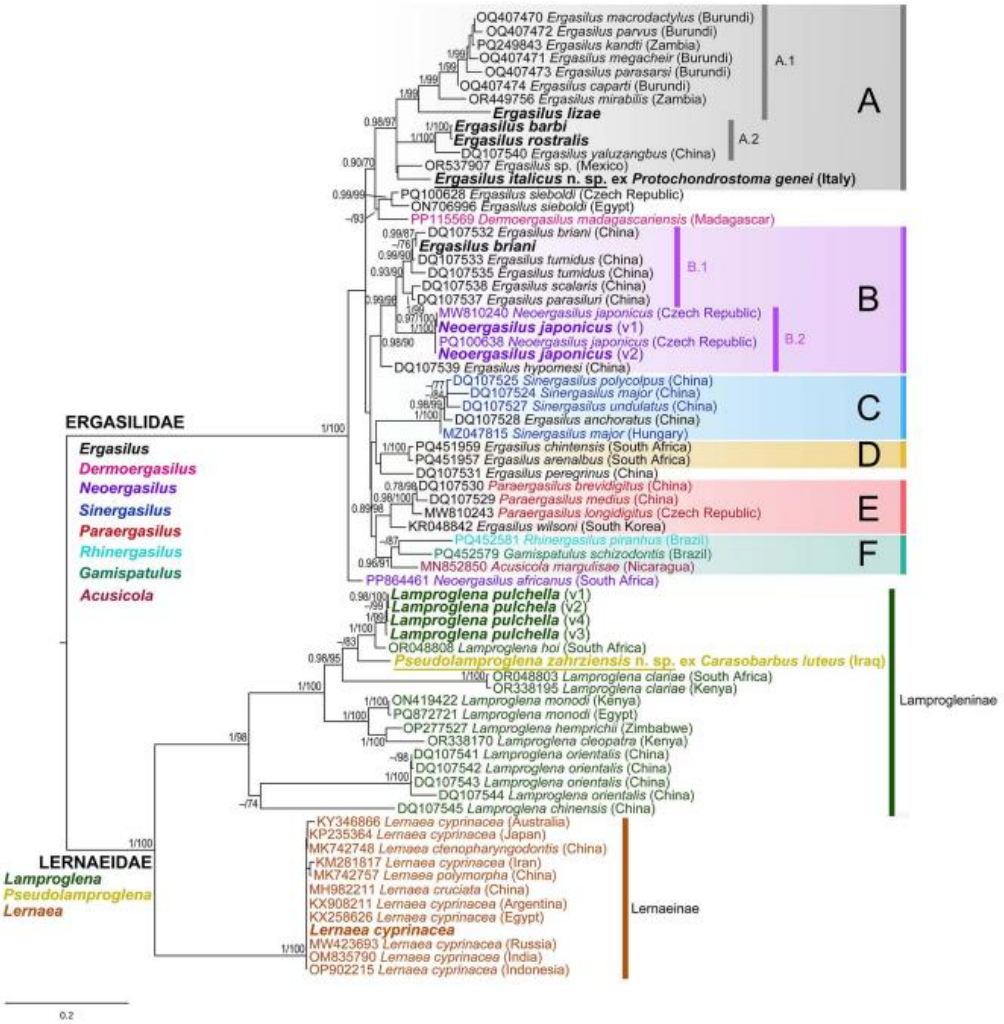


Figure 11. Phylogenetic tree of Ergasilidae and Lernaeidae reconstructed by Maximum Likelihood. The tree is based on the partial 28S rDNA sequences. Values along the branches indicate posterior probabilities from Bayesian Inference and bootstrap values from Maximum Likelihood (dashes indicate values below 0.7 and 50, respectively). New sequences are in bold and newly described species are underlined. Detailed information about localities and accession numbers are given in Table 3.

(*E. mirabilis*), the Chinese species *Ergasilus yaluzangbus* Kuang & Qian, 1985, and unidentified species of *Ergasilus* from the endemic *Floridichthys polyommus* Hubbs, 1936 in the Yucatán Peninsula. *Ergasilus lizae* was placed in a basal position within the African subclade A.1., *E. barbi* and *E. rostralis* formed a well-supported subclade A.2 (BI = 1; ML = 100) with the Chinese species *E. yaluzangbus*, positions of the new described species *E. italicus* n. sp. and an unidentified Mexican species were unresolved within clade A. The species of *Ergasilus briani* and *N. japonicus* were included in clade B, *E. briani* together with 3 other Chinese species (*E. tumidus*, *Ergasilus scalaris* Markevich, 1940 and *Ergasilus parasiluri* (Yamaguti, 1936)) formed subclade B.1 (BI = 0.99; ML = 99), and two genetic variants of *N. japonicus* from Mediterranean and Middle East were included in subclade B.2 (BI = 1; ML = 100).

Within Lernaeidae, species were formed by 2 big clades, corresponding to subfamilies Lamprogleninae and Lernaeinae (BI = 1; ML = 100). All observed genetic variants of *L. pulchella* and the new described species *P. zahrziensis* n. sp. clustered together with African species *Lamproglena hoi* Dippenaar, Luus-Powell & Roux, 2001 and *Lamproglena clariae* Fryer, 1956 (BI = 0.98; ML = 95).

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The newly obtained sequence of *L. cyprinacea* was placed with others *L. cyprinacea* sequences isolated from diverse fish hosts from different parts of world and Chinese species *Lernaea cruciata* (Lesueur, 1824), *L. ctenopharyngodontis* and *Lernaea polymorpha* (Yü, 1938) (BI = 1; ML = 100).

Discussion

In the present study, parasitic copepods were recorded on 60 fish host species across 9 countries. These findings, which include the identification of 10 species from six genera, contribute to the growing knowledge of parasitic copepod diversity in the Mediterranean and Middle East regions. Comparisons with previous records of 30 species belonging to 6 genera of Ergasilidae and 10 species of 3 genera of Lernaeidae in the Mediterranean and Middle Eastern regions reveal both consistencies and novel findings.

Within the Ergasilidae, 7 species representing 3 genera were found, with the highest species richness observed for the genus *Ergasilus*. No species were recorded from the genera *Dermoergasilus, Mugillicola* and *Nipergasilus* that had previously been reported in Mediterranean areas and Iraq. From the 19 previously described *Ergasilus* species in the Mediterranean and Middle Eastern regions, only *E. barbi, E. briani, E. lizae* and *E. rostralis* were found in this study.

Ergasilus briani was found to be the most prevalent and abundant species, exhibiting the widest distribution range. In this study, its presence has been recorded for the first time in Bosnia and Herzegovina, Croatia, Albania and Greece. However, the Mediterranean regions have historically been under-sampled for fish parasites. Recent records of this species in North Macedonia, Algeria or Turkey (Alas et al., 2015; Berrouk et al., 2020, 2022; Blazhekovikj-Dimovska and Stojanovski, 2022), combined with the present findings, suggest a broader distribution range than previously assumed. No specimens have yet been detected in the Iberian or Apennine peninsulas. *Ergasilus briani* was originally described by Markevich (1933) from Russia (then the USSR) and has since been documented across much of the Palearctic region. Parasitic females of this species predominantly infest various cyprinid fishes, typically residing on the inner side of the gill filaments (Alston et al., 1993). Our morphological identification of specimens of *E. briani* matched the most recent redescription by Alston et al. (1996). Additionally, molecular comparison with Chinese specimens deposited in the GenBank database [DQ107572 (18S), DQ107532 (28S); Song et al., 2008] showed high similarity (99.71% for 18S, 98.51% for 28S).

Ergasilus barbi, previously confirmed only in Iraq, was now recorded at 5 localities in Turkey, with the highest abundance found on *Barbus escherichii* (Steindachner, 1897) in Kütahya (a total of 165 specimens recorded on 5 host specimens). It was originally described by Rahemo (1982) from *Arabibarbus grypus* (Heckel, 1843) in the Tigris River near Mosul, Iraq. In the same study, morphologically very similar *E. mosulensis* was also described. Ho et al. (1996) later provided a redescription due to discrepancies between their collected specimens and the original paratypes. The only difference between the two species is a presence of an outer spine on the second exopod segment of leg 1 in *E. barbi* (*vs* absence in *E. mosulensis*). Until now, *E. barbi* had not been recorded outside of Iraq. However, given that *E. mosulensis* has previously been reported in Atatürk Dam Lake, Turkey (Jawad and Öktener, 2007; Öktener et al., 2007, 2008; Öktener and Alaş, 2009; Öktener, 2021), it is plausible that both species may have expanded from Iraq. Nevertheless, comprehensive morphological and molecular analyses are recommended to reliably differentiate *E. barbi* from *E. mosulensis* and to avoid possible misidentification, especially given that no molecular data are currently available for *E. mosulensis*.

The findings of *Ergasilus rostralis* in low abundances at 2 localities in Iraq are in accordance with its previous geographical records. It was first discovered on coastal water fishes from Kerala, India on three species of grey mullet in Veli Lake (estuarine), Trivandrum and in Neendakara (estuarine), Quilon (Ho et al., 1992). Later, it was recorded from the Shatt Al-Arab River, Basrah Province, Iraq, where it is currently known to infect 20 species of both fresh and marine fish (Ho et al., 1996; Al-Daraji and Mhaisen, 2023; Mhaisen and Al-Daraji, 2023). Phylogenetic analysis revealed a close relationship with *E. barbi*, suggesting that both species may have originated in Iraq or close area. The occurrence of *E. rostralis* in India could be a secondary introduction or expansion, but molecular data from India are still lacking.

In this study, *E. lizae* was recorded only in Greece, which represents the second record of this species in the country (Ragias et al., 2005). In the Mediterranean and Middle East areas, it was previously reported from several countries. Generally, *E. lizae* is considered an almost cosmopolitan species, primarily restricted to fish hosts from the family Mugilidae, but it is not highly host-specific and may also infect other fish species such as cichlids, eels or cyprinids, especially when they occur in the same area as mullets (Paperna, 1975). *Ergasilus lizae* was first reported by Krøyer (1863) from the gills of the mullet in USA (New Orleans), although no drawings were provided. Later, Ben Hassine and Raibaut (1980) synonymised *Ergasilus nanus* Beneden, 1870 with *E. lizae* even though Kabata (1979) concluded, based on a comparison of his specimens with Roberts (1970) description, that they are distinct species. *Ergasilus lizae* was redescribed by Kabata (1992) from specimens from Australia and most recently from Mexico (Morales-Serna and Camacho-Zepeda, 2024). In our sampling, the morphology of specimens of *E. lizae* was more consistent with the former descriptions of Kabata (1992) instead of the redescription from Mexico. Moreover, some authors claim *E. lizae* to be a marine species (Morales-Serna and Camacho-Zepeda, 2024), while others report it from brackish waters (Paperna, 1975; Yalım et al., 2023) or even freshwater (Kabata, 1992). We identified *E. lizae* in the Sperchios River (near the village of Ypati), which has over 60 tributaries and forms a large delta before emptying into the Maliakos Gulf, ultimately reaching the Aegean Sea (Piria et al., 2018). In this river, which is influenced by seawater, salinity levels in the estuarine area can fluctuate, creating brackish conditions that may be suitable for *E. lizae*. In addition, El-Rashidy (1999) suggested that *E. lizae* might also represent a complex of cryptic species with similar morphology. The discrepancies among authors regarding whether it is marine or freshwater species, as well as synonymization of *E. nanus,* might actually support this hypothesis of cryptic species complex. The phylogenetic analyses revealed a close relationship between *E. lizae* and African *Ergasilus* species, including *E. kandti*, a species recorded from the upper parts of Egypt, which belongs to the Mediterranean and Middle East region. This finding could suggest a possible evolutionary or biogeographical link between African and Mediterranean species.

The new described species, *E. italicus* n. sp., is the first description of a new species of Ergasilidae in Europe in this century. Only 4 specimens were found on the gills of the endemic fish *Protochondrostoma genei*, distributed in Italy and Slovenia. Previously, only 3 known species of the genus *Ergasilus* (*E. lagunaris, E. lizae* and *E. sieboldi*) were recorded in Italy

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(Grandori, 1925; Aisa et al., 1983; Lui et al., 2013). Additionally, an unidentified *Ergasilus* sp. was used in the study examining mast cell responses (Dezfuli et al., 2011). However, neither morphological nor molecular data were provided to support its identification. Based on the single photo it is difficult to presume which species it might be, but it does not appear to match *E. italicus* n. sp. *Ergasilus lagunaris* was described from the Venetian Bay in 1925 (Grandori, 1925), but it was documented on a single occasion and has not been referenced since. The description of *E. lagunaris* is outdated and only based on a male specimen, which should not be a standard for describing new species of parasitic copepods. Both *E. lizae* and *E. sieboldi* from Scardovari Lagoon and Lake Trasimeno have also been recorded on a single occasion only. There is a considerable lack of scientific papers on ergasilids or lernaeids from Italy, and our discovery may indicate the potential for further new records from this area. Phylogenetic analyses confirmed the inclusion of *E. italicus* n. sp. in clade A, which includes the African *Ergasilus* species, *E. barbi, E. lizae, E. rostralis, E. yaluzangbus* and unidentified *Ergasilus* sp. from Mexico, but its closer relationship with these species was not supported.

From 2 *Neoergasilus* species previously recorded in the Mediterranean and Middle East, *N. japonicus* was recorded in this study from 14 host species of the Leuciscidae and Cyprinidae in Italy, Croatia, Turkey and Iraq. *Neoergasilus japonicus* was originally described from Taiwan in Lake Jitsugetsutan (Harada, 1930) as *Ergasilus japonicus* (Harada, 1930) from cyprinid fishes, but later transferred by Yin (1956) to the genus *Neoergasilus*. This species is native to eastern Asia, including Taiwan, China, Japan, Korea and the Russian Far East (Nagasawa and Uyeno, 2012). Since its discovery it has spread throughout the world, often introduced along with live fishes and exhibits extremely low host specificity (Suárez-Morales et al., 2010) and is currently classified as an invasive parasite (Ondračková et al., 2024, 2025). Our new geographical records in Croatia and Iraq further support the hypothesis that *N. japonicus* is readily dispersed, likely through natural water flows, fish translocations, or human-mediated activities. Present results suggest that its current distribution is likely underestimated, with a potential for even wider dissemination than currently documented. Phylogenetic reconstruction confirmed its placement in clade B with the closest relationships with ergasilids from China (Song et al., 2008). For both rDNA sequences, 2 types of genetic variants were found, which is consistent with the findings of Ondračková et al. (2019). However, no morphological differences were observed, and it might only be a case of intraspecific variability due to introduction from various places on multiple occasions. Genetic data are currently available for only two species of this genus, namely *N. japonicus*, which forms a monophyletic well-supported group within clade B, and the newly described *Neoergasilus africanus* (Fikiye et al., 2024) parasitizing *Clarias gariepinus* (Burchell, 1822) in South Africa (Fikiye et al., 2024), which has been placed at the base of an entire clade of Ergasilidae, raising doubts about the monophyly of the genus.

Only 1 species of the genus *Paraergasilus*, namely *P. longidigitus* has been found for the first time in Albania with very low abundances (3 specimens overall). In the studied areas, it was previously documented only from *Alburnus alburnus* (Linnaeus, 1758) in Turkey (Koyun et al., 2007). In the Palearctic region, it is a widely distributed species, typically inhabiting the nasal cavity of fish. This specific localization may lead to its underreporting if dissections are not conducted thoroughly. In general, the members of the genus *Paraergasilus* are known for their low host specificity, with over 20 cyprinid species identified as hosts, while some species are also capable of parasitising bivalve molluscs (Chernysheva and Purasjoki, 1991). Unfortunately, we were unable to obtain any molecular data for *P. longidigitus* due to drying off of fixed specimens during long-term storage, but the morphological examination and comparison matched the most recent study of Kvach et al. (2021).

Within Lernaeidae, only 3 species belonging to 3 genera were recorded in this study. *Lernaea cyprinacea* was found in both adult and copepodid forms in various stages of the life cycle in Portugal, Spain, Italy, Croatia, Bosnia and Herzegovina and Turkey, thereby confirming its extensive distribution in these regions and very low host specificity. It is one of the most recognized parasitic copepods and is currently regarded as a cosmopolitan species with a broad geographic distribution, spanning North and South America, Europe, Asia, Southern Africa and Australia (Avenant-Oldewage, 2012). No intraspecific variability was observed in our dataset, and all available genetic sequences of *Lernaea* species are strikingly similar. The phylogenetic analysis suggests that *L. cruciata, L. ctenopharyngodontis* and *L. polymorpha* are not genetically distinct from *L. cyprinacea*. This observation raises doubts about the distinctiveness of these *Lernaea* species, suggesting that they may not be separate species, but rather variations of a single, widely distributed species, *L. cyprinacea*, with greater intraspecific genetic variability. Another possible explanation is that the rDNA genetic markers, commonly used for phylogenetic analysis and delimitation of species of Lernaeidae, may not provide enough information to accurately distinguish species within *Lernaea*. Moreover, several *Lernaea* species have previously been synonymized with *L. cyprinacea* (e.g., *Lernaea carassii* Tidd, 1933 and *Lernaea elegans* Leigh-Sharpe, 1925) (Harding, 1950) and multiple subspecies have also been described in the past (Yü, 1938; Hu, 1948; Gnanamuthu, 1951).

In the Mediterranean and Middle Eastern regions, *L. pulchella* was previously recorded only from Italy, Iraq and Turkey and now it was found as adults on 20 different host species across Italy, Bosnia and Herzegovina, Greece and Turkey. It is presumably the only *Lamproglena* species occurring in Europe, with a distribution extending across most of the Palearctic region, reaching as far as Iraq (Rahemo and Ami, 2013), and with its most recent discovery in North Macedonia (Blazhekovikj-Dimovska and Stojanovski, 2024). Even though this species appears to be quite uniform in its morphological traits, several discrepancies between the original description and later records have been observed. The molecular analysis of *L. pulchella* revealed the presence of 4 distinct but closely related 28S rDNA genetic variants, suggesting that this taxon may represent a complex of cryptic species rather than a single species. Despite genetic variation, individuals exhibited highly similar morphological traits, with only minor differences observed in their overall size. Specimens were collected from multiple locations and fish hosts, with main differences between sequences from Turkey and European countries. This may highlight the necessity for further studies to clarify the taxonomic status of *L. pulchella* and potentially new species might have to be described in the future. Since no distinct morphological traits were observed for the description of new species, we identify all of them as *L. pulchella*.

The newly described species, *P. zahrziensis* n. sp., is the third species of genus *Pseudolamproglena* recorded from Iraq, following *P. annulata* and *P. boxshalli*, and the fifth within the genus, distinguished by several unique morphological features. The genus *Pseudolamproglena* appears to be geographically restricted to the Middle and Far East, but it has rarely been reported outside of Iraq since its initial description and does not seem to exhibit high

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prevalence or dispersal tendencies. The genus *Pseudolamproglena* is distinguished from *Lamproglena* mainly by distinctive somatic segmentation and the structure and armature of the maxillae and maxillipeds (Boxshall, 1976). The molecular data obtained in this study represent the first genetic records for this genus. Molecular analysis placed *P. zahrziensis* n. sp. firmly within the family Lernaeidae, clustering closely with sequences of *L. pulchella* from the Middle East and Mediterranean, as well as *L. hoi* from South Africa. The close phylogenetic relationship between *P. zahrziensis* n. sp. and species of *Lamproglena* suggests that the members of *Pseudolamproglena* may not represent a distinct genus, but instead could be highly modified copepods within the *Lamproglena* clade. However, further molecular data, particularly from additional *Pseudolamproglena* species and other members of the *Lamproglena* clade, are necessary to resolve this issue definitively. Until more comprehensive genetic analyses are available, the status of *Pseudolamproglena* as a separate genus remains uncertain. It is possible that future studies will reveal that *Pseudolamproglena* should be synonymized with *Lamproglena*.

Conclusion

This study provides new insights into the distribution and taxonomy of parasitic copepods in the Mediterranean and the Middle East, expanding known host ranges and identifying new localities for several species. The findings underscore the importance of continued research on these parasites, as their diversity and biogeographical patterns remain underexplored. Molecular analyses revealed significant phylogenetic challenges within the families Ergasilidae and Lernaeidae, particularly regarding the polyphyletic nature of *Ergasilus* and the uncertain species boundaries in the genera *Lernaea* and *Lamproglena*. The study suggests that taxonomic revisions are necessary, potentially requiring the reclassification of some genera. Comprehensive morphological and molecular studies are needed to resolve taxonomic uncertainties and assess the true diversity and distribution of these parasitic copepods.

Supplementary material. The supplementary material for this article can be found at https://doi.org/10.1017/S0031182025100814.

Data availability statement. Type and voucher specimens were deposited in the Institute of Parasitology, Czech Academy of Sciences, České Budějovice, Czech Republic (accession codes IPCAS Cr-40 and IPCAS Cr-41). The sequences produced in this study were deposited in GenBank of NCBI at https://www.ncbi.nlm.nih.gov/ (accession codes PX000625-PX000680; PV988324-PV988349).

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Author contributions. RM and MS conceived and designed the study. RM, AŠ, MB and MS collected parasitological material, RM performed morphological characterization and described the species, RŠ and JV collected fishes. RM and MS performed molecular and phylogenetic analyses. IH performed SEM. RM and MS wrote the first draft of the manuscript. All authors substantially contributed to the final draft and approved the final version of the manuscript.

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Competing interests. The authors declare there are no conflicts of interest.

Ethical standards. All applicable institutional, national and international guidelines for the care and use of animals were followed. This study was approved by the Animal Care and Use Committee of the Faculty of Science, Masaryk University in Brno (Czech Republic).

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Paper 4 (unpublished manuscript)

Míč, R. & Seifertová, M. (2026). Global diversity of Ergasilidae and Lernaeidae.

Global diversity of parasitic copepods from families Ergasilidae and Lernaeidae

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Abstract

Freshwater parasitic copepods belonging to the cyclopoid families Ergasilidae and Lernaeidae represent widespread and economically significant parasites of fishes. However, their global diversity and distribution have not previously been synthesised within a single, standardised framework. This review compiles and evaluates published records from original descriptions to the present, integrating taxonomic status, host associations, biogeographical occurrence, and available molecular data. A total of 284 valid species of Ergasilidae assigned to 29 genera and 126 valid species of Lernaeidae assigned to 18 genera are recognised worldwide. Ergasilids have been recorded from at least 55 host orders, 152 host families, and more than 750 host species, while lernaeids parasitise at least 32 host orders, 78 host families, and more than 470 fish species, with occasional records from amphibians. Twelve ergasilid species are known exclusively from planktonic material and have not been recorded from hosts. Species richness exhibits strong geographical structuring. Ergasilidae have their highest diversity in the Neotropical region (102 species, 19 genera), followed by the Oriental (75 species) and Palaearctic (72 species) regions. In contrast, Lernaeidae are most diverse in the Oriental (58 species) and Afrotropical (43 species) regions. Host-use patterns are uneven in both families, with cypriniform fishes dominating host records. Broad host generalism is limited to a small number of widely distributed taxa, notably the invasive *Neoergasilus japonicus* and *Lernaea cyprinacea*, the latter has been recorded from more than 270 host species. Molecular data remain limited (47 ergasilid species; 13 lernaeid species), supporting the polyphyly of *Ergasilus* and highlighting unresolved generic boundaries, but still insufficient for major taxonomic restructuring. Selected nomenclatural and taxonomic adjustments are formalised to stabilise usage and standardise the global checklist.

Key words: parasitic copepods**;** biogeography; Ergasilidae; Lernaeidae; diversity; phylogeny

Key Findings

- the first global review of Ergasilidae and Lernaeidae

Introduction

Freshwater parasitic copepods represent one of the major groups of crustacean parasites. Among those placed within the Cyclopoida, the families Ergasilidae Burmeister, 1835 and Lernaeidae Cobbold, 1879 include some of the most widespread and economically significant ectoparasites of fishes, causing gill pathology, impaired respiratory function, secondary infections and substantial losses in wild populations and aquaculture. Both families display high levels of morphological and biological diversification, broad host associations, and complex attachment strategies that are central to their evolutionary success and biogeographical dispersal (Kabata, 1979; Boxshall & Defaye, 2008; Avenant-Oldewage, 2012; Boxshall & Hayes, 2019; Hadfield *et al*., 2025).

Ergasilidae currently contains 29 valid genera, with *Anklobrachius* Thatcher, 1999 regarded as *genus inquirendum* (Boxshall & Halsey, 2004). Adult females are typically parasitic on fishes, but the genus *Teredophilus* Rancurel, 1954 and *Paraergasilus rylovi* Markevich, 1937 are parasites of freshwater bivalves (Markevich, 1937; Rancurel, 1954). Males and all developmental stages from nauplius through to adult are free-living components of planktonic communities (Kabata, 1979; Izawa, 1987; Boxshall & Defaye, 2008). In some freshwater or estuarine systems, free-living ergasilid stages may be abundant or even dominant components of local plankton assemblages (Boxshall & Defaye, 2008). Ergasilids may cause haemorrhaging and severe gill damage at the site of attachment or facilitate secondary infections (Piasecki *et al*., 2004). Heavy infections can result in impaired respiration, abnormal swimming behaviour and mortality (Lester & Hayward, 2006). Ergasilids have also been implicated as potential disease vectors or reservoir hosts for viral pathogens (Nigrelli, 1950; Jones & Hine, 1983; Overstreet *et al*., 2009).

Lernaeidae represents one of the most highly specialised parasitic lineages of cyclopoid copepods and currently contains 18 valid genera. The family is characterised by pronounced sexual dimorphism. Adult males retain a cyclopiform body plan and are short-lived, typically dying soon after mating. Fertilised females undergo a marked post-mating metamorphosis. During this transformation, the cephalothorax and associated appendages are modified into specialised attachment structures that either anchor deeply within host tissues or function as ectoparasitic organs on the gills (Boxshall & Hayes, 2019; Hadfield *et al*., 2025). Lernaeids comprise two principal morphological groups corresponding with historic subfamilies:

Lamprogleninae, which attach ectoparasitically to the gills via enlarged maxillae, and Lernaeinae, which anchor mesoparasitically within tissues using a metamorphosed anterior holdfast (Boxshall & Halsey, 2004). Holdfast morphology in *Lernaea* is notoriously plastic and influenced by tissue microenvironment, producing wide intraspecific variability that has historically complicated species delimitations (Harding, 1950). Species of *Lernaea* burrow into the skin of its host fish and can cause disease called lernaeosis where haemorrhagic ulcers occur at the attachment side. Death of the host can occur due to the secondary infections and severe bleeding (Khalifa & Post, 1976; Kabata, 1984).

Despite their widespread distributions and substantial economic relevance, no comprehensive global synthesis of Ergasilidae and Lernaeidae has been undertaken that integrates diversity, host ranges, and historical biogeography. Existing records remain scattered across continents, host families, and taxonomic traditions, with most species originally described on the basis of morphology alone, often from brief or outdated accounts. Recent regional surveys and integrative morphological and molecular studies have revealed previously unrecognised diversity, overlooked host associations, and persistent problems with generic boundaries and monophyly (e.g., Amado *et al*., 1995; Ho, 1998; Boxshall & Halsey, 2004; Míč *et al*. 2023, 2024, 2025; Narciso *et al*., 2025).

Here we compile, standardise and analyse all available published records of Ergasilidae and Lernaeidae from their original descriptions to the present. A standardized global database also provides a necessary foundation for future molecular phylogenetics and revision of several genera and species. Together, these data establish the first comprehensive global context for the taxonomy, evolution and host ecology of Ergasilidae and Lernaeidae.

Materials and methods

A comprehensive global dataset of valid species of Ergasilidae and Lernaeidae was compiled from all original descriptions, redescriptions, parasite surveys, taxonomic revisions, regional checklists and parasitological reports published from the mid-eighteenth century to the present. Literature searches were conducted using published monographs, Web of Science, Google Scholar and online databases (mainly WoRMS/World of Copepods). For each record, species identity, host taxon (order, family, species), geographic locality and site of infection were extracted and cross-checked against original descriptions whenever possible. Where competing descriptions existed, only verified or redescribed information was retained. Nomenclature of parasite species followed WoRMS and recent systematic literature (Boxshall & Halsey, 2004). Host nomenclature was standardised using FishBase, and historical host names were traced to

current valid combinations. Ambiguous or unverifiable host-parasite associations were excluded from analyses if key diagnostic traits were missing, were inconsistent with the generic diagnosis, or were unsupported by voucher specimens. Species with unclear identity, uncertain validity, unresolved synonymies or marked as *species inquirendae* or *nomina dubia*, were excluded and are listed under Supplementary Table 1 Notes. Host range was assessed at family and genus level of the hosts. Records of non-fish hosts, including bivalves and amphibians were included. Biogeographical analyses followed a realm-based structure by Boxshall & Defaye (2008) using standard freshwater ecoregion definitions, with species richness measured independently for the Neotropics, Afrotropics, Palaearctic, Oriental, Australasian, Nearctic, Pacific Ocean Island and Antarctic regions. Molecular data were gathered from widely used databases GenBank and BOLD.

Results

Global diversity of Ergasilidae and Lernaeidae

A total of 284 valid species of Ergasilidae assigned to 29 genera and 126 valid species of Lernaeidae assigned to 18 genera were recognised globally during this study. Ergasilid parasites were recorded from at least 55 host orders, 152 host families and more than 750 host species, with the vast majority reported from freshwater, estuarine or marine actinopterygian fishes and a small number of additional records from elasmobranchian fishes (*Ergasilus myctarothes* Wilson, 1913; *Ergasilus ogawai* Kabata, 1992 and *Ergasilus trygonophilus* Domingues & Marques, 2010) and bivalves (genus *Teredophilus* Rancurel, 1954 and *Paraergasilus rylovi* Markevich, 1937). Overall, 12 ergasilid species are known solely from plankton collections and have never been recorded from any host, despite displaying clear morphological adaptations for parasitism in the form of characteristic prehensile antennae. These include *Acusicola minuta* Araujo & Boxshall, 2001; *Ergasilus bani* Ohtsuka, Ho & Nagasawa, 2004; *Ergasilus chautauquaensis* Fellows, 1887; *Ergasilus divergens* (Kokubo, 1914); *Ergasilus foresti* Boxshall, Araujo & Montu, 2002; *Ergasilus genuinus* (Kokubo, 1914); *Ergasilus lagunaris* Grandori, 1925; *Ergasilus longicaudatus* Kuang & Li, 1984; *Ergasilus sergipensis* Amado & Rocha, 2001; *Paraergasilus reductus* Ranga Reddy & Kasaiah, 1994; *Pseudovaigamus spinicephalus* (Thatcher & Robertson, 1984); and *Vaigamus retrobarbatus* Thatcher & Robertson, 1984. At least 19 species of *Ergasilus* have been reported from marine habitats, although the separation of freshwater, brackish and marine occurrences is frequently ambiguous in the literature, especially for estuarine and lagoonal records (Tang & Kalman, 2008; van der Spuy *et al*., 2025).

Lernaeid copepods are recorded from at least 32 host orders and 78 host families and more than 470 individual fish species, while *Lernaea cyprinacea* Linnaeus, 1758 is also occasionally reported on amphibian hosts (Waicheim *et al*., 2019; MacHale & Hedley, 2021; Varga *et al*., 2024). With the sole exception of *Lamproglena lichiae* von Nordmann, 1832 and dubious record of *Lamproglena notopterai* Jafri & Mahar, 2006, which has been reported from a marine fish, all lernaeids parasitise freshwater hosts (Piasecki, 1993; Kunutu *et al*., 2018).

The geographical distribution of valid species and genera recognised in this study is summarised in Table 1, Fig. 1 (Ergasilidae) and Table 2, Fig. 2 (Lernaeidae), arranged according to the eight major biogeographical regions. The highest ergasilid species richness occurs in the Neotropical (102 species/19 genera) and Oriental regions (75/8), followed by the Palaearctic (72/8), Afrotropical (33/8) and Nearctic (33/6) regions, and comparatively reduced richness in the Australasian (20/8) and Pacific Ocean Island (2/2) regions. Lernaeidae exhibit a different regional pattern with a stronger concentration of species in Oriental (58/9) and Afrotropical (43/7) drainages, with less species richness in Palaearctic (19/3), Neotropical (13/8), Nearctic (8/1) and Australasian regions (2/1). Several genera, including *Ergasilus*, *Lamproglena* and *Lernaea*, exhibit almost cosmopolitan distributions and occur in multiple biogeographical regions, whereas multiple other genera are regionally restricted.

A complete species level account including valid and synonymized names, hosts, distribution records is provided in Supplementary Tables 1 and 2. To ensure consistency across regions, the checklist excludes subspecies, male-based genus (*Anklobrachius*) and nominal species lacking adequate descriptions or diagnostic material. The tables already include taxonomical changes listed below. Several historical names were treated as *nomina dubia* or *genera inquirenda* following established revisions. Full justification for individual exclusions and taxonomic decisions is provided in Notes for Supplementary Table S1.

Table 1 Number of Ergasilidae species recorded per biogeographical region, total number of currently valid species and type of hosts (some species may be present in more geographical regions)

Taxon	PA	NA	NT	AT	OL	AU	PAC	ANT	Valid species	Hosts
Ergasilidae Burmeister, 1835	**72**	**33**	**102**	**33**	**75**	**20**	**2**	**0**	**284**	
Abergasilus Hewitt, 1978	–	–	–	–	–	1	–	–	1	Actinopterygii
Acusicola Cressey, 1970	–	1	17	–	–	–	–	–	18	Actinopterygii, plankton
Amplexibranchius Thatcher & Paredes, 1985	–	–	1	–	–	–	–	–	1	Actinopterygii
Brasergasilus Thatcher & Boeger, 1983	–	–	6	–	–	–	–	–	6	Actinopterygii
Dermoergasilus Ho & Do, 1982	3	–	–	4	7	5	–	–	14	Actinopterygii
Duoergasilus Narciso, Brandão, Perbiche-Neves & da Silva, 2019	–	–	1	–	–	–	–	–	1	Actinopterygii
Ergasilus von Nordmann, 1832	49	28	45	19	46	7	1	–	165	Actinopterygii, Elasmobranchii, plankton
Gamidactylus Thatcher & Boeger, 1984	–	–	4	–	–	–	–	–	4	Actinopterygii
Gamispatulus Thatcher & Boeger, 1984	–	–	2	–	–	–	–	–	2	Actinopterygii
Gamispinus Thatcher & Boeger, 1984	–	–	1	–	–	–	–	–	1	Actinopterygii
Gauchergasilus Montú & Boxshall, 2002	–	–	1	–	–	–	–	–	1	Actinopterygii
Majalincola Tang & Kalman, 2008	–	–	–	–	–	1	–	–	1	Actinopterygii
Miracetyma Malta, 1993	–	–	3	–	–	–	–	–	3	Actinopterygii
Mugilicola Tripathi, 1960	2	–	–	1	1	1	–	–	4	Actinopterygii
Neoergasilus Yin, 1956	5	1	1	2	7	1	–	–	11	Actinopterygii
Nipergasilus Yamaguti, 1939	1	–	–	1	2	–	–	–	2	Actinopterygii
Paeonodes Wilson C.B., 1944	–	1	–	1	–	1	1	–	4	Actinopterygii
Paraergasilus Markevich, 1937	7	1	–	3	8	3	–	–	16	Actinopterygii, Bivalvia, plankton
Pindapixara Malta, 1995	–	–	1	–	–	–	–	–	1	Actinopterygii
Prehendorastrus Boeger & Thatcher, 1990	–	–	2	–	–	–	–	–	2	Actinopterygii
Pseudovaigamus Amado, Ho & Rocha, 1995	–	–	2	–	–	–	–	–	2	Actinopterygii, plankton
Rhinergasilus Boeger & Thatcher, 1988	–	–	3	–	–	–	–	–	3	Actinopterygii
Sinergasilus Yin, 1949	3	–	–	–	3	–	–	–	3	Actinopterygii
Teredophilus Rancurel, 1954	–	–	–	2	–	–	–	–	2	Bivalvia
Therodamas Krøyer, 1863	–	–	8	–	–	–	–	–	8	Actinopterygii
Thersitina Norman, 1905	2	1	–	–	1	–	–	–	2	Actinopterygii

Tiddergasilus Marques & Boeger, 2018	–	–	2	–	–	–	–	–	2	Actinopterygii
Urogasilus Rosim, Boxshall & Ceccarelli, 2013	–	–	1	–	–	–	–	–	1	Actinopterygii
Vaigamus Thatcher & Robertson B.A., 1984	–	–	1	–	–	–	–	–	1	plankton
Anklobrachius Thatcher, 1999*	–	–	1	–	–	–	–	–	1	plankton

PA: Palaearctic, NA: Nearctic, NT: Neotropical, AT: Afrotropical, OL: Oriental, AU: Australasian, PAC: Pacific Oceanic Islands, ANT: Antarctic; **genus inquirendum* (not accounted)

Table 2 Number of Lernaeidae species recorded per biogeographical region, total number of currently valid species and type of hosts (some species may be present in more geographical regions)

Taxon	PA	NA	NT	AT	OL	AU	PAC	ANT	Valid species	Hosts
Lernaeidae Cobbold, 1879	**19**	**8**	**13**	**43**	**58**	**2**	**0**	**0**	**126**	
Lamprogleninae Sproston, Yin & Hu, 1950	**12**	–	**1**	**21**	**33**	**0**	**0**	**0**	**61**	
Afrolernaea Fryer, 1956	–	–	–	6	–	–	–	–	6	Actinopterygii
Catlaphilla Tripathi, 1960	–	–	–	–	2	–	–	–	2	Actinopterygii
Indolernaea Kabata, 1983	–	–	–	–	4	–	–	–	4	Actinopterygii
Indopeniculus Kumari, Khera & Gupta, 1988	–	–	–	–	2	–	–	–	2	Actinopterygii
Lamproglena von Nordmann, 1832	9	–	1	14	22	–	–	–	40	Actinopterygii
Lamproglenoides Fryer, 1964	–	–	–	1	1	–	–	–	2	Actinopterygii
Pseudolamproglena Boxshall, 1976	3	–	–	–	2	–	–	–	5	Actinopterygii
Lernaeinae Wilson C.B., 1917	**7**	**8**	**12**	**22**	**25**	**2**	**0**	**0**	**65**	
Amazolernaea Thatcher & Williams, 1998	–	–	1	–	–	–	–	–	1	Actinopterygii
Areotrachelus Wilson C.B., 1924	–	–	1	–	–	–	–	–	1	Actinopterygii
Bedsylernaea Thatcher & Williams, 1998	–	–	1	–	–	–	–	–	1	Actinopterygii
Dysphorus Kurtz, 1924	–	–	–	1	–	–	–	–	1	Actinopterygii
Lernaea Linnaeus, 1758	7	8	4	16	22	2	–	–	48	Actinopterygii, Amphibia
Lernaeogiraffa Zimmermann, 1923	–	–	–	1	–	–	–	–	1	Actinopterygii
Minilernaea Thatcher & Huergo, 2005	–	–	1	–	–	–	–	–	1	Actinopterygii
Opistholernaea Yin, 1960	–	–	–	4	1	–	–	–	5	Actinopterygii
Perulernaea Thatcher & Paredes, 1985	–	–	2	–	–	–	–	–	2	Actinopterygii
Pillainus Kabata, 1983	–	–	–	–	2	–	–	–	2	Actinopterygii
Taurocheros Brian, 1924	–	–	2	–	–	–	–	–	2	Actinopterygii

PA: Palaearctic, NA: Nearctic, NT: Neotropical, AT: Afrotropical, OL: Oriental, AU: Australasian, PAC: Pacific Oceanic Islands, ANT: Antarctic

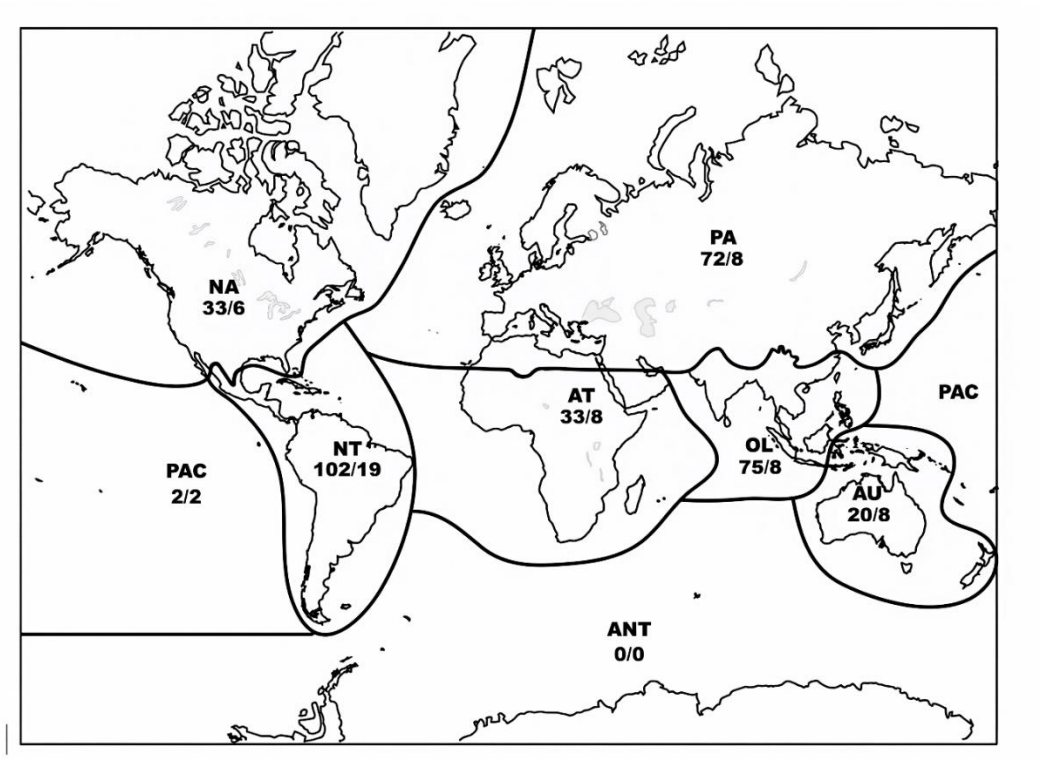


Fig. 1.: Geographical distribution of species and genera of Ergasilidae (species number/ genus number), coded according to the main zoogeographic regions. PA: Palaearctic, NA: Nearctic, NT: Neotropical, AT: Afrotropical, OL: Oriental, AU: Australasian, PAC: Pacific Oceanic Islands, ANT: Antarctic (regional scheme adapted from Boxshall & Defaye, 2008).

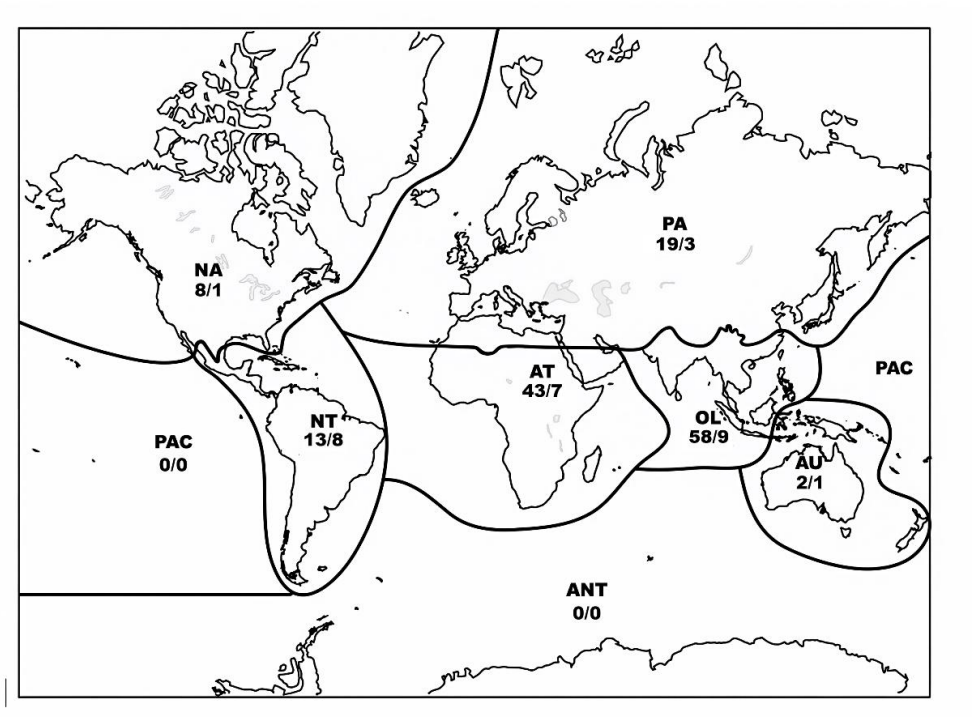


Fig. 2.: Geographical distribution of species and genera of Lernaeidae (species number/g number), coded according to the main zoogeographic regions. PA: Palaearctic, NA: Nearctic, NT: Neotropical, AT: Afrotropical, OL: Oriental, AU: Australasian, PAC: Pacific Oceanic Islands, ANT: Antarctic (regional scheme adaptedfrom Boxshall & Defaye, 2008).

Note: The Palaearctic-Oriental boundary in southern China is difficult to define because the transition between temperate and subtropical zones is gradual and many Chinese records lack precise geographic coordinates, often listing only counties or large regional names. This vagueness complicates biogeographic assignment, but several southern Chinese localities clearly fall within the Oriental region. These include Lianjiang County in Guangdong, Baisha in Jiangyou County in Sichuan, multiple sites in Yunnan such as Mengding and Baoshan, localities in Guizhou such as Songtao and Yinjiang, and all records from Hainan Island, which is entirely Oriental in biogeographic affinity. The entire Qinghai-Tibet Plateau (including the Lhasa, Niyong, and Nianchu river basins) is classified as Palaearctic due to its cold montane cyprinid assemblages and historical connection to Central Asian and Siberian faunas rather than to Oriental lowland drainages.

Regional patterns in Ergasilidae and Lernaeidae

Species of Ergasilidae are cosmopolitan, with representatives in freshwater, brackish waters and marine environment in all major zoogeographic regions except of Antarctica and with peak diversity in the Neotropics, where more than half of all currently recognised genera are endemic. By contrast, the Lernaeidae are globally widespread but restricted almost entirely to freshwater systems and are absent from the Pacific Oceanic Islands and Antarctica. Their highest species richness occurs in the Old World, particularly in Asian (Oriental) and African (Afrotropical) drainages, which together form the principal centres of lernaeid diversification.

Palaearctic region

The Palaearctic region contains 72 ergasilid species distributed among 8 genera. The fauna is strongly dominated by *Ergasilus* (49 species), which accounts for most regional records (Fig. 3). Additional genera include *Paraergasilus* (7), *Neoergasilus* (5), *Dermoergasilus* (3), *Sinergasilus* (3), *Mugilicola* (2), *Thersitina* (2) and *Nipergasilus* (1). Many Palaearctic records derive from cypriniform and other temperate freshwater fishes and occur predominantly in freshwater, with a smaller number recorded from brackish or coastal environments. For Lernaeidae, the Palaearctic region supports 19 valid species, primarily belonging to the genera *Lamproglena* (9) and *Lernaea* (7), with additional records from *Pseudolamproglena* (3) (Fig. 4). No endemic genera occur in the region, and most Palaearctic species are widely distributed Old World taxa. The Palearctic nonetheless forms one of the principal distributional centres of Lernaeidae, representing the northernmost limit of the family and providing extensive host and locality records for widely distributed species.

Host representation in the Palearctic ergasilid fauna reflects the structure of local ichthyofaunas and long-term sampling in Eurasian freshwater systems (Fig. 5). Cypriniformes dominate all records, followed by Siluriformes, Mugiliformes, and Gobiiformes, while numerous additional orders appear as sparse, isolated occurrences. Lernaeid host representation

follows an even steeper cypriniform bias, supplemented by Perciformes, Cyprinodontiformes, Siluriformes, Anabantiformes, and miscellaneous scattered orders. These patterns represent the composition of heavily sampled host families, particularly cyprinids and leuciscids, rather than any evolved host specificity.

Taxonomic work on freshwater parasitic copepods in the Palaearctic has has the longest historical continuity of any region. Foundational descriptions were produced in the 18th and 19th centuries by European naturalists (e.g. Linnaeus, 1758; von Nordmann, 1832; Krøyer, 1863; Heller, 1865). A second major era began in the early 20th century and continued across several decades in the former Soviet Union, which generated extensive regional monographs and many new species descriptions (Markevich, 1933, 1937, 1940, 1946, 1956; Dogiel & Akhmerov, 1952). Parallel taxonomic activity in China and Japan produced complementary reports of *Ergasilus*, *Sinergasilus*, *Paraergasilus*, *Lernaea* and *Lamproglena* (Yü, 1937, 1938; Yin, 1949, 1960; Yamaguti, 1936, 1939; Kuang, 1977; Kuang & Qian, 1991). Descriptive and taxonomic work in the Palearctic reached its highest intensity between the 1950s and the 1990s, a period marked by extensive regional monographs and comprehensive faunal treatments (e.g. Kabata, 1979; Fryer & Andrews, 1983; Alston *et al*., 1993, 1996). Subsequent research has focused primarily on invasive species, range extensions and molecular confirmation of established taxa (e.g. Kvach *et al*., 2021, 2024; Ondračková *et al*., 2025a). New species still appear occasionally, and long-term sampling has produced comprehensive regional survey for the Mediterranean and Middle East (Míč *et al*., 2025).

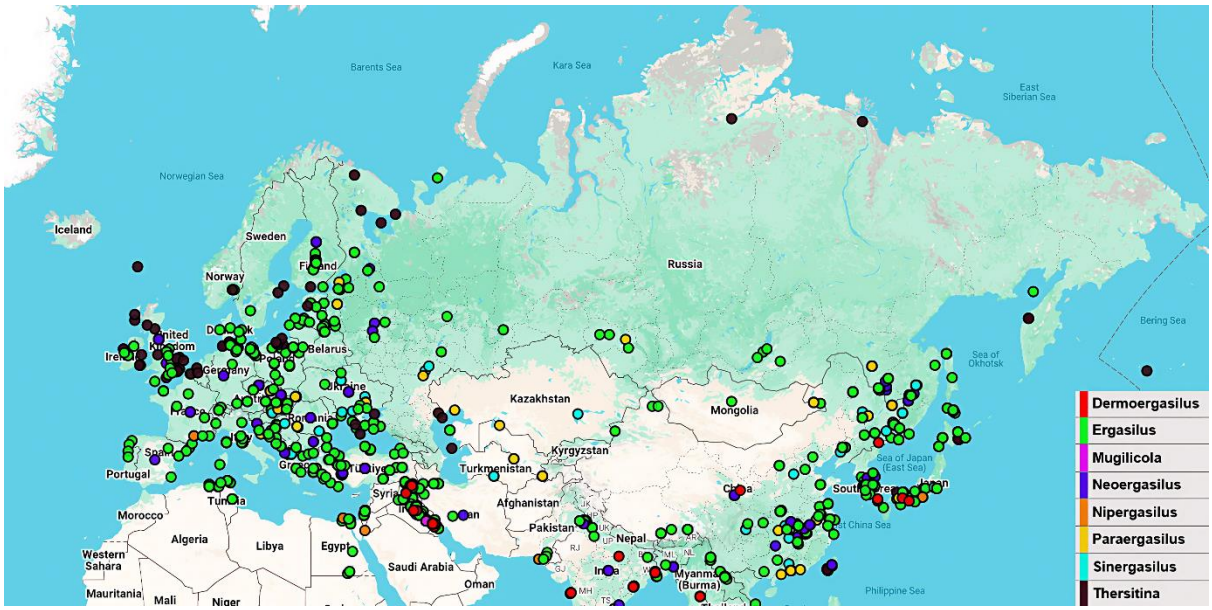


Figure 3. Locality records of Ergasilidae in the Palaearctic region, colour-coded by genus.

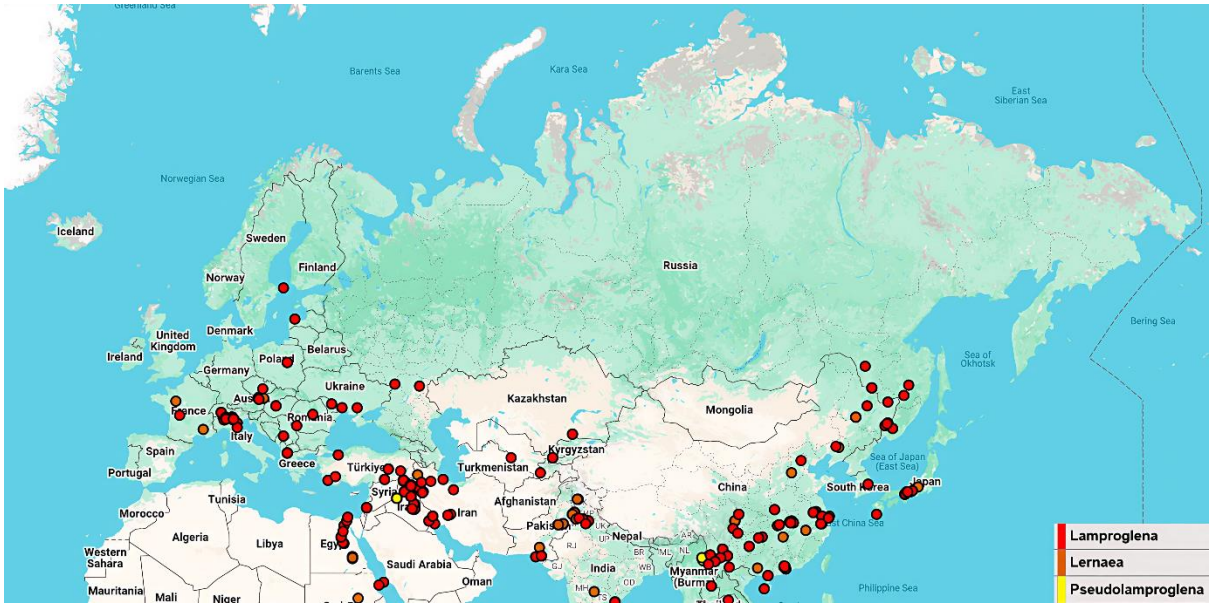


Figure 4. Locality records of Lernaeidae in the Palaearctic region, colour-coded by genus.

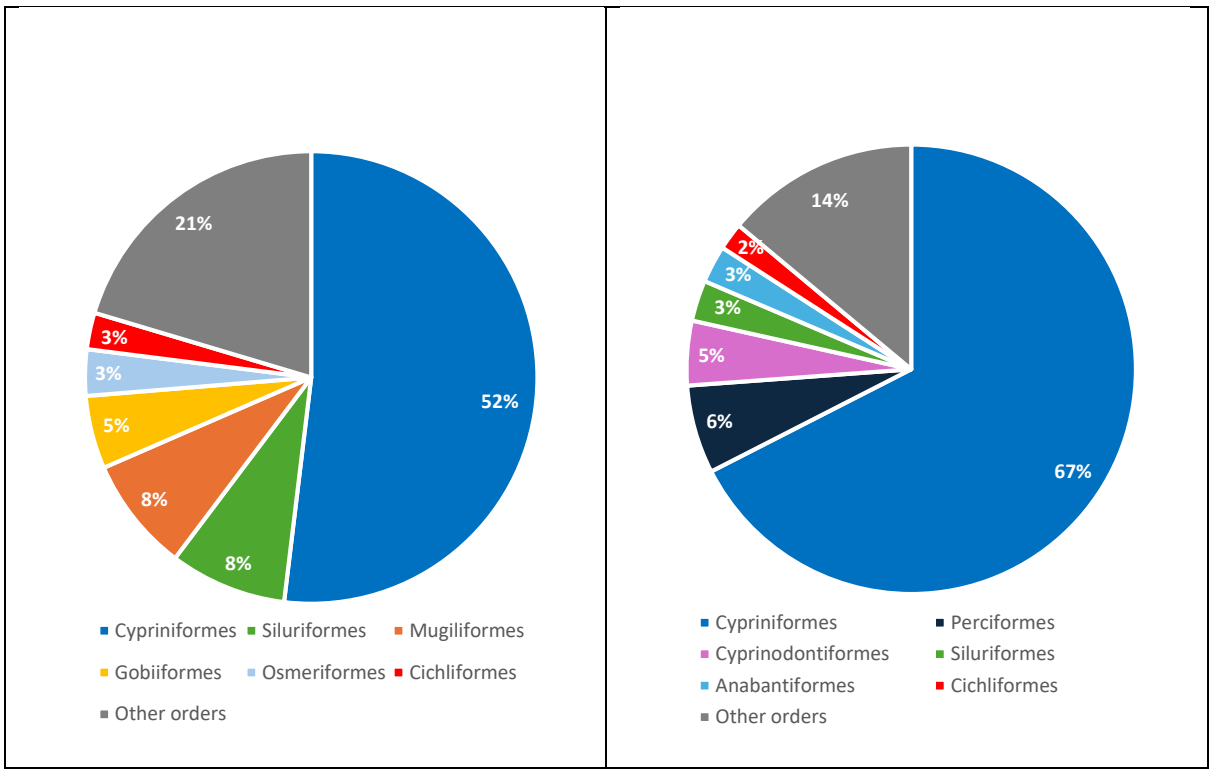


Figure 5. Relative representation of host orders in Palaearctic ergasilid (a) and lernaeid (b) records; minor categories are aggregated as "other orders". Percentages expressed as proportions of total host records.

Oriental region

The Oriental region contains 75 ergasilid species belonging to 8 genera. As in the Palaearctic, the fauna is dominated by *Ergasilus* (46), supplemented by *Paraergasilus* (8), *Dermoergasilus* (7), *Neoergasilus* (7), *Sinergasilus* (3), *Nipergasilus* (2), *Mugilicola* (1) and

Thersitina (1) (Fig. 6). For Lernaeidae, the Oriental region comprises 57 valid species in 9 genera and represents one of the key centres of diversity for the family (Fig. 7). In addition to the widely distributed *Lernaea* (22) and *Lamproglena* (22), the region contains 4 endemic genera, *Catlaphilla* (2), *Indolernaea* (4), *Indopeniculus* (2) and *Pillainus* (2). Further records include *Pseudolamproglena* (2) and a single species of *Lamproglenoides* (1) and *Opistholernaea* (1). The concentration of both generic and species diversity in this region is most likely a result of early radiation associated with Asian cypriniform lineages (Ho, 1998).

Host representation in Oriental ergasilid records is dominated by Cypriniformes, which account for more than one third of all host records, followed by Mugiliformes and Siluriformes. Additional records occur across Cichliformes, Beloniformes, Acanthuriformes, Anabantiformes, Centrarchiformes and several minor orders. Lernaeid records are even more strongly dominated by Cypriniformes, supplemented by Siluriformes, Anabantiformes and Osteoglossiformes, with small contributions from Cyprinodontiformes, Cichliformes and a few additional orders. These proportions reflect both the structure of regional fish faunas and the strong sampling focus on Asian cyprinids since the mid-twentieth century, especially across India, China and Southeast Asia (Fig. 8).

Early descriptions were geographically patchy and often associated with European expeditions to India and Southeast Asia (Southwell & Prashad, 1918; Capart, 1941, 1943), alongside the first contributions by regional authors (Velasquez, 1951; Redkar *et al*., 1952; Karamchandani, 1953; Tripathi, 1960). A substantial expansion followed between the 1970s and 1990s, driven by systematic work in India and expanding survey coverage in Southeast Asia (Cressey & Collette, 1970; Kabata, 1983; Kumari *et al*., 1988; Battish & Brar, 1989; Ho *et al*., 1992; Ho & Kim, 1997). Later revisions and descriptions by El-Rashidy & Boxshall (2000, 2001a, 2002) refined generic limits and added new species, particularly in *Dermoergasilus*, *Paraergasilus* and *Mugilicola*. Recent decades have seen an increase in local surveys across Pakistan, India, Sri Lanka, Vietnam and other Southeast Asian countries. These studies have contributed valuable distributional data and occasional new records, although some identifications were based on limited material and may require revision (e.g. Jafri & Mahar, 2006; Tasawar *et al*., 2007; Sarmila *et al*., 2023). Despite the comparatively rich record, many eastern and insular parts of the realm, especially Borneo, Sulawesi and the Philippines, remain insufficiently sampled.

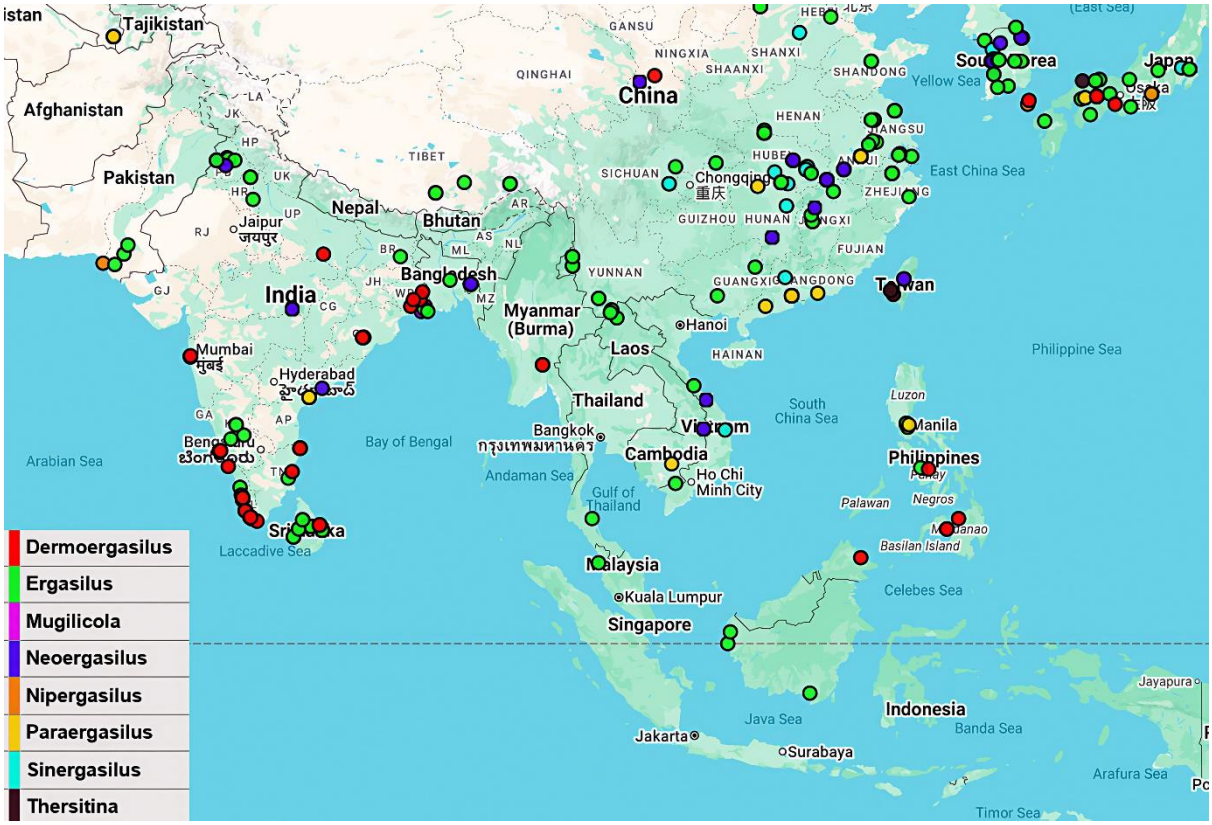


Figure 6. Locality records of Ergasilidae in the Oriental region, colour-coded by genus.

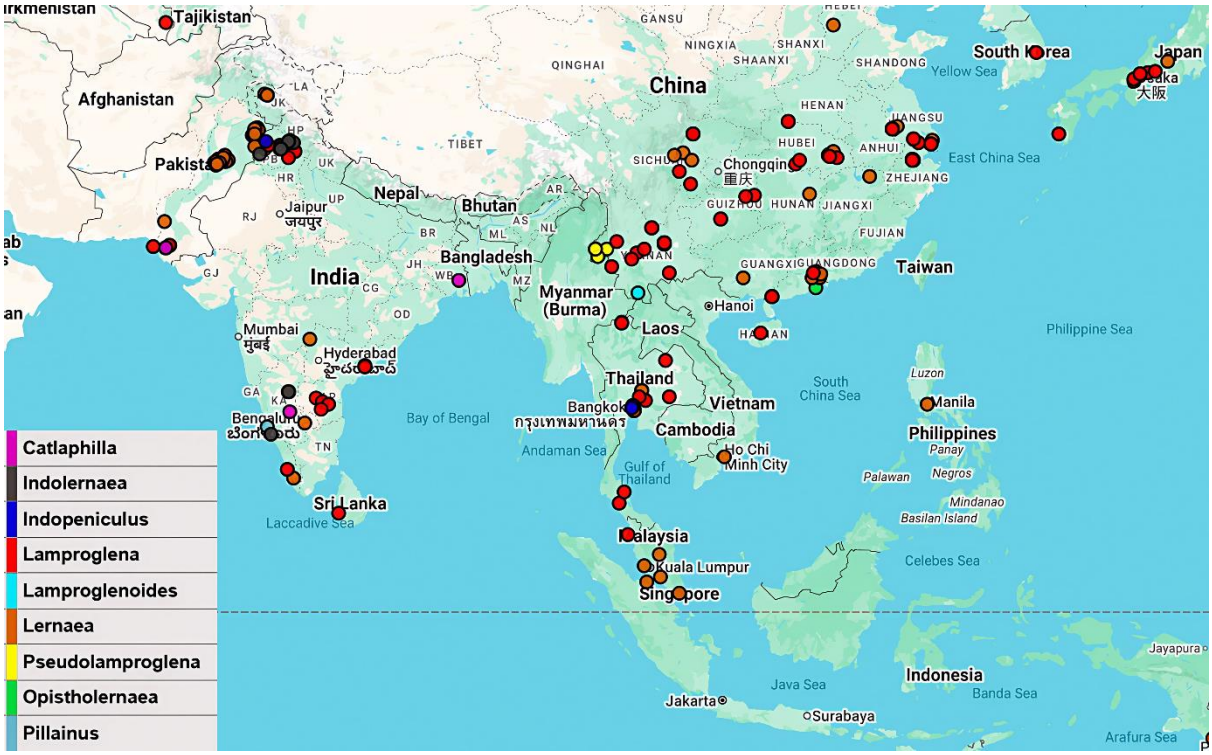


Figure 6. Locality records of Lernaeidae in the Oriental region, colour-coded by genus.

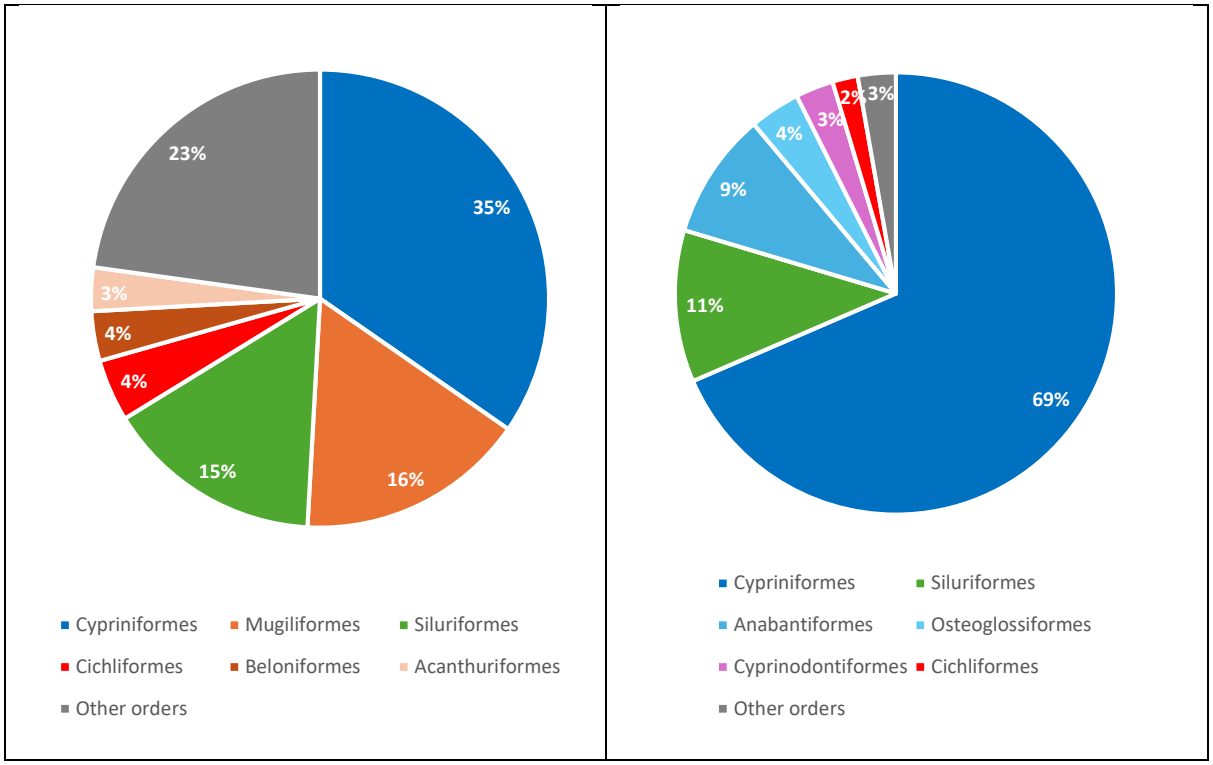


Figure 7. Relative representation of host orders in Oriental ergasilid (a) and lernaeid (b) records; minor categories are aggregated as "other orders". Percentages expressed as proportions of total host records.

Afrotropical region

The Afrotropical region currently records 33 ergasilid species in 8 genera. The fauna is dominated by *Ergasilus* (19), with additional representatives of *Dermoergasilus* (4), *Mugilicola* (1), *Neoergasilus* (2), *Nipergasilus* (1), *Paeonodes* (1), *Paraergasilus* (3) and the bivalve associated genus *Teredophilus* (2) (Fig. 8). In contrast to the Palaearctic and Oriental regions, *Thersitina* is absent and *Teredophilus* is endemic to the Afrotropics. As in the other Old World regions, *Ergasilus* accounts for most records, whereas the remaining genera are each represented by few species and usually by limited locality data. For Lernaeidae, the Afrotropical region contains 43 valid species in 7 genera and supports the endemic genera *Afrolernaea* (6), *Dysphorus* (1) and *Lernaeogiraffa* (1), in addition to the diversified *Lamproglena* (14) and *Lernaea* (16), with further species of *Opistholernaea* (4) and *Lamproglenoides* (1) (Fig. 9). The majority of African species occur in association with cichlids, cyprinids and other regionally dominant freshwater hosts and represent a southern extension of the principal Asian-African radiation.

Host representation in Afrotropical ergasilid records is concentrated in Cichliformes, which account for nearly half of all host occurrences, followed by Siluriformes, Osteoglossiformes,

Mugiliformes and Characiformes. Additional records are scattered across Cypriniformes and a wide array of less frequently sampled orders. Lernaeid records show a similar structure, where Cichliformes again dominate, supplemented by Cypriniformes, Siluriformes, Characiformes, Osteoglossiformes, Polypteriformes and a few additional orders represented by small numbers of records. These distributions describe the composition of available host records and primarily reflect the dominance of cichlids, cyprinids and characiforms in African freshwaters and the historical focus of parasitological work on these groups, rather than any strict limitation of host range (Fig. 10).

Early records of ergasilid and lernaeid copepods were sparse and derived mainly from West Africa and the Nile basin (Sars, 1909; Cunnington, 1914; Monod, 1924; Brian, 1927; Capart, 1944). A major expansion followed in the mid-twentieth century with detailed studies on East African cichlids, which first revealed the high diversity of ergasilid and lernaeid parasites in the Great Lakes (Harding, 1950; Fryer, 1956, 1959, 1960, 1961, 1964, 1967, 1968). Broad regional surveys across the Nile and West African systems further increased the known fauna (Dollfus, 1960; Paperna, 1968, 1969, 1980; Thurston, 1970; Shotter, 1978; Paperna & Overstreet, 1981). After a period of relative inactivity, new descriptions and redescriptions from Lake Tanganyika and other East African systems renewed interest in the region (Míč *et al*., 2023). In southern Africa, research has been continuous since the late 1980s and has produced important redescriptions, new species and molecular data (Oldewage & van As, 1987, 1988; Killian & Avenant-Oldewage, 2013; Pretorius & Avenant-Oldewage, 2023; Rindoria *et al*., 2023; van der Spuy *et al*., 2025; Pretorius *et al*., 2025). Large parts of central and western Africa remain poorly sampled, and present species richness is most likely still underestimated.

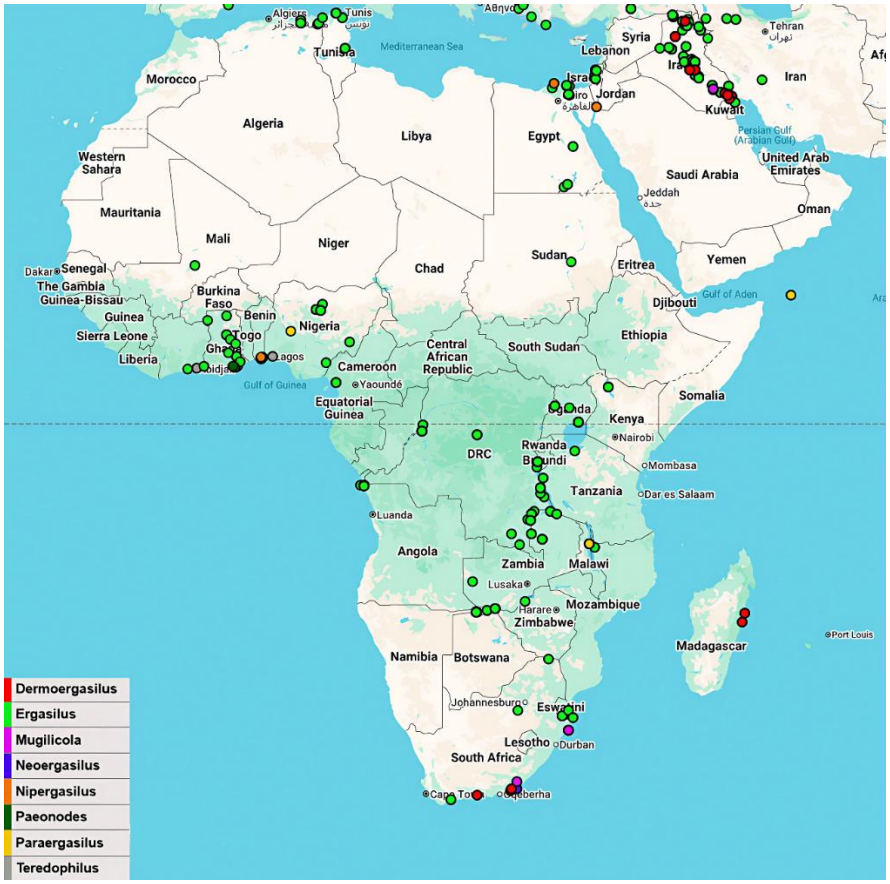


Figure 8. Locality records of Ergasilidae in the Afrotropical region, colour-coded by genus.

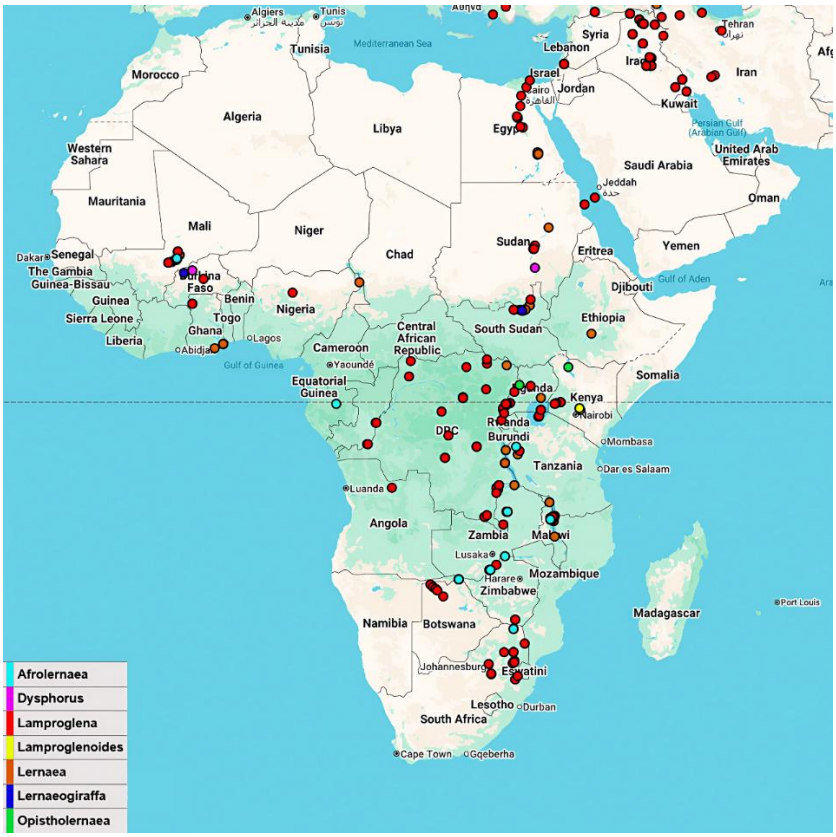


Figure 9. Locality records of Lernaeidae in the Afrotropical region, colour-coded by genus.

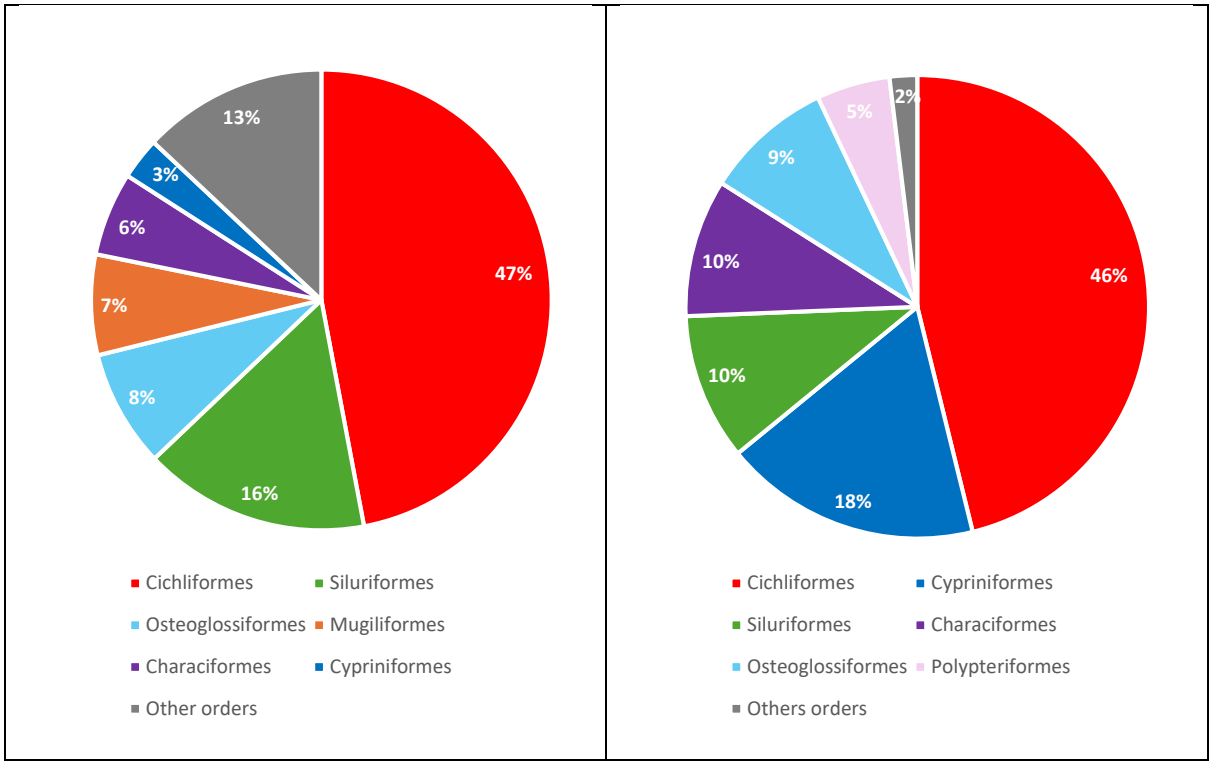


Figure 10. Relative representation of host orders in Afrotropical ergasilid (a) and lernaeid (b) records; minor categories are aggregated as "other orders". Percentages expressed as proportions of total host records.

Neotropical region

The Neotropical region contains 102 valid ergasilid species, representing the highest diversity recorded for any biogeographical realm. These species are distributed among 19 genera, 16 of which are endemic to South and Central American freshwater systems. Endemic genera include *Amplexibranchius* (1), *Brasergasilus* (6), *Duoergasilus* (1), *Gamidactylus* (4), *Gamispatulus* (2), *Gamispinus* (1), *Gauchergasilus* (1), *Miracetyma* (3), *Pindapixara* (1), *Prehendorastrus* (2), *Pseudovaigamus* (2), *Rhinergasilus* (3), *Therodamas* (8), *Tiddergasilus* (2), *Urogasilus* (1) and *Vaigamus* (1) (Fig. 11). Furthermore, *Acusicola* (16) has expanded northward through Central America, and a single species has reached as far as Texas in the Nearctic. Despite that, the fauna is still dominated by *Ergasilus* (45) and the last representative is an introduced species of *Neoergasilus* (1). The high diversity of the region corresponds with the exceptional diversity of South American freshwater fishes and the long independent history of the Neotropical ichthyofauna. For Lernaeidae, the Neotropical region includes 13 valid species, distributed among 8 genera, of which 6 are endemic: *Amazolernaea* (1), *Areotrachelus* (1), *Bedsylernaea* (1), *Minilernaea* (1), *Perulernaea* (2) and *Taurocheros* (2) (Fig. 12). Additionally, species of *Lernaea* (4) and a single introduced species of *Lamproglena* (1) has been recorded.

Host representation reflect the structure of Neotropical ichthyofaunas (Fig. 13). Nearly half of all ergasilid host records derive from Characiformes, followed by Mugiliformes, Siluriformes and Cichliformes. Additional records span Clupeiformes, Beloniformes, Cyprinodontiformes and a range of minor orders. Lernaeid records show a similar structure, with Characiformes dominating, followed by Cichliformes and Siluriformes, and a few occurrences among Centrarchiformes and Cypriniformes.

Early records were sparse and inconsistent (Brian, 1903, 1924, 1944), and a coherent taxonomic framework did not exist until the late twentieth century. A period of rapid expansion began in the 1980s, when intensive fieldwork across Brazil and neighbouring countries produced numerous new species and established most endemic Neotropical genera (Thatcher, 1981, 1984; Thatcher & Robertson, 1984; Thatcher & Boeger, 1983, 1984; Thatcher & Paredes, 1985a,b; Boeger & Thatcher, 1990; Malta, 1993, 1994; Malta & Varella, 1995; Varella & Malta, 1996; Amado & Rocha, 1996; El-Rashidy & Boxshall, 1999). Survey and taxonomic activity continued into the early 2000s, including large faunal inventories and basin-wide studies in the Amazon and Paraná systems (Amado & Rocha, 2001; Araujo & Boxshall, 2001; Guidelli *et al*., 2006; Lacerda *et al*., 2007; Tavares & Luque, 2007; Takemoto *et al*., 2009). A second wave of descriptions followed after 2010, driven by expanded regional sampling, new host records and the introduction of molecular data into Neotropical parasitic copepod systematics (e.g. Rosim *et al*., 2013; Murrieta-Morey *et al*., 2016; Taborda *et al*., 2016; Varella *et al*., 2019; Narciso *et al*., 2019, 2020a,b, 2025; Santacruz *et al*., 2020; Waicheim *et al*., 2021; Couto *et al*., 2023). Despite this progress, large parts of Amazonia, the Guiana Shield, western Amazon tributaries and the south parts of the region remain inadequately sampled, and true diversity is likely to exceed current estimates.

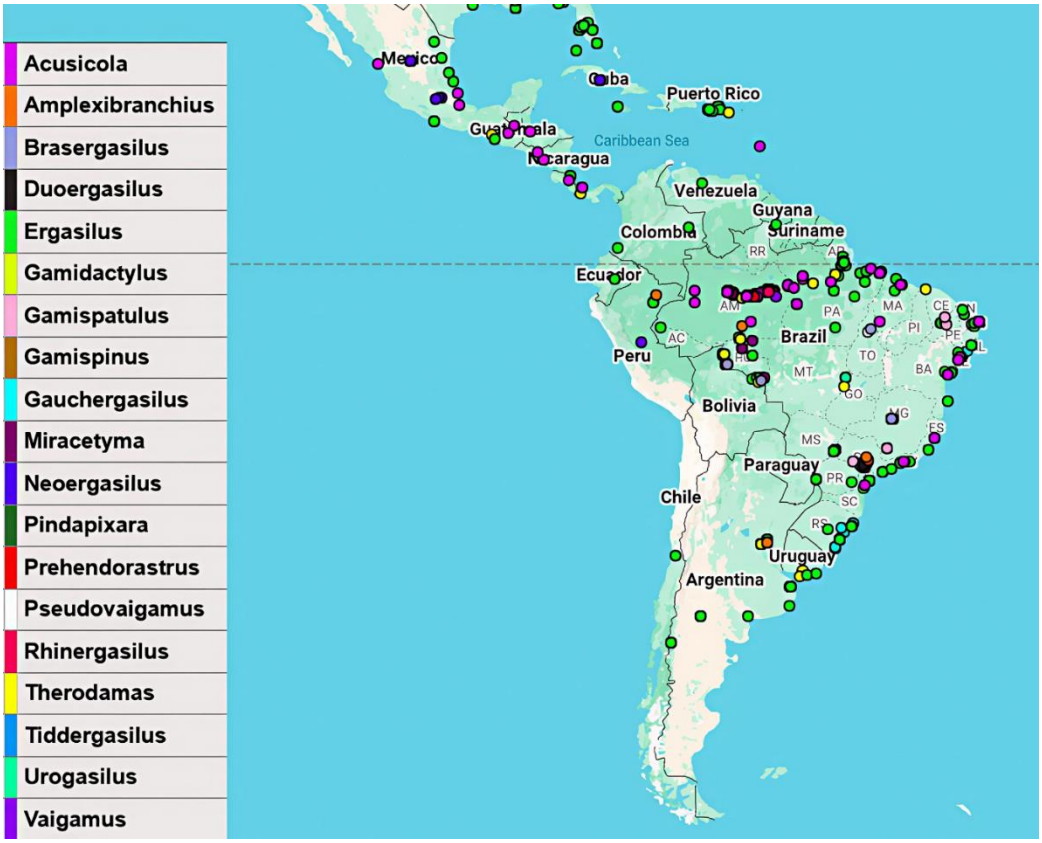


Figure 11. Locality records of Ergasilidae in the Neotropical region, colour-coded by genus.



Figure 12. Locality records of Lernaeidae in the Neotropical region, colour-coded by genus.

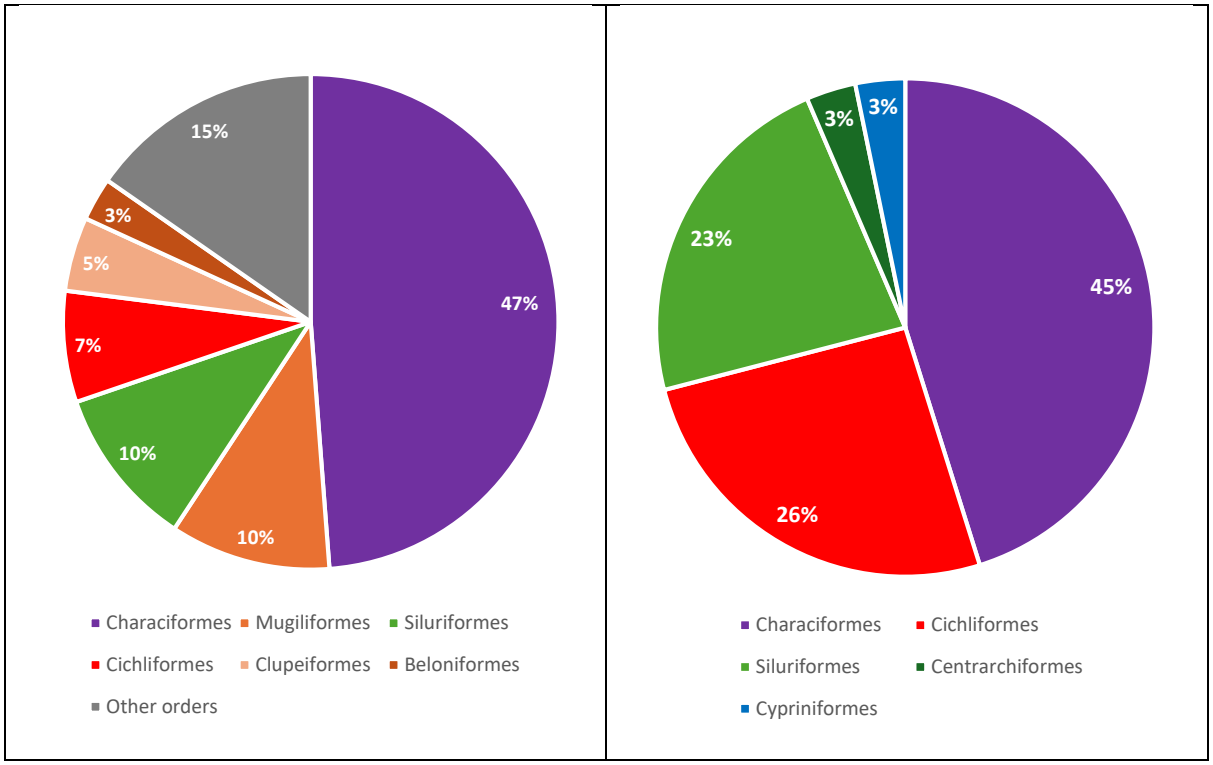


Figure 13. Relative representation of host orders in Neotropical ergasilid (a) and lernaeid (b) records; minor categories are aggregated as "other orders". Percentages expressed as proportions of total host records.

Nearctic region

The Nearctic region contains 33 valid ergasilid species distributed among 6 genera. The fauna is strongly dominated by *Ergasilus* (28), with single representatives of *Acusicola* (1), *Neoergasilus* (1), *Paeonodes* (1), *Paraergasilus* (1) and *Thersitina* (1) (Fig. 14). No genus is endemic to the region. Species richness is comparatively low and reflects both the restricted host diversity of temperate North American freshwater systems and the limited historical intensity of parasitic copepod sampling outside major fisheries and aquaculture areas. For Lernaeidae, the Nearctic fauna comprises 8 valid species, all assigned to *Lernaea* (8) (Fig. 15). No endemic lernaeid genera occur in the region.

Host representation in Nearctic ergasilids is led by Cypriniformes and Centrarchiformes, followed by Salmoniformes, Siluriformes and Cyprinodontiformes. Additional records occur across several percomorph suborders and other minor orders. Lernaeid records are dominated by Centrarchiformes and Cypriniformes, followed by Siluriformes and small numbers from Eupercaria and a few additional orders, reflecting the structure of North American freshwater fish assemblages and the taxonomic focus of past sampling efforts (Fig. 16).

Taxonomic work on Nearctic parasitic copepods began in the late nineteenth century with scattered descriptions from the United States and Canada (Kellicott, 1881; Wright, 1882; Fellows, 1887). More substantial work followed in the early to mid-twentieth century, notably through the extensive contributions of Wilson (1911, 1916, 1917, 1924, 1932, 1944), whose descriptions and redescriptions established the basis for Nearctic taxonomy. A major expansion occurred between the 1960s and early 1990s through surveys in the Great Lakes, Mississippi basin and both coasts, which added several species, revised most of the species and clarified host associations (Roberts, 1963, 1965, 1969a,b, 1970; Johnson & Rogers, 1972, 1973; Margolis & Kabata, 1988; Hudson *et al*., 1994). After the 1990s, descriptive output declined, and recent work has focused primarily on documenting invasive species and aquaculture-associated introductions, especially *L. cyprinacea* and *N. japonicus* (e.g. Hayden & Rogers, 1998; Hudson & Bowen, 2002; Suárez-Morales & Mercado-Salas, 2013; Truong & Bullard, 2021). These records dominate modern Nearctic parasitic copepod literature, yet expanded sampling of native freshwater fishes remains necessary to resolve several persistent taxonomic ambiguities within *Ergasilus* and to clarify the true extent of regional species diversity.

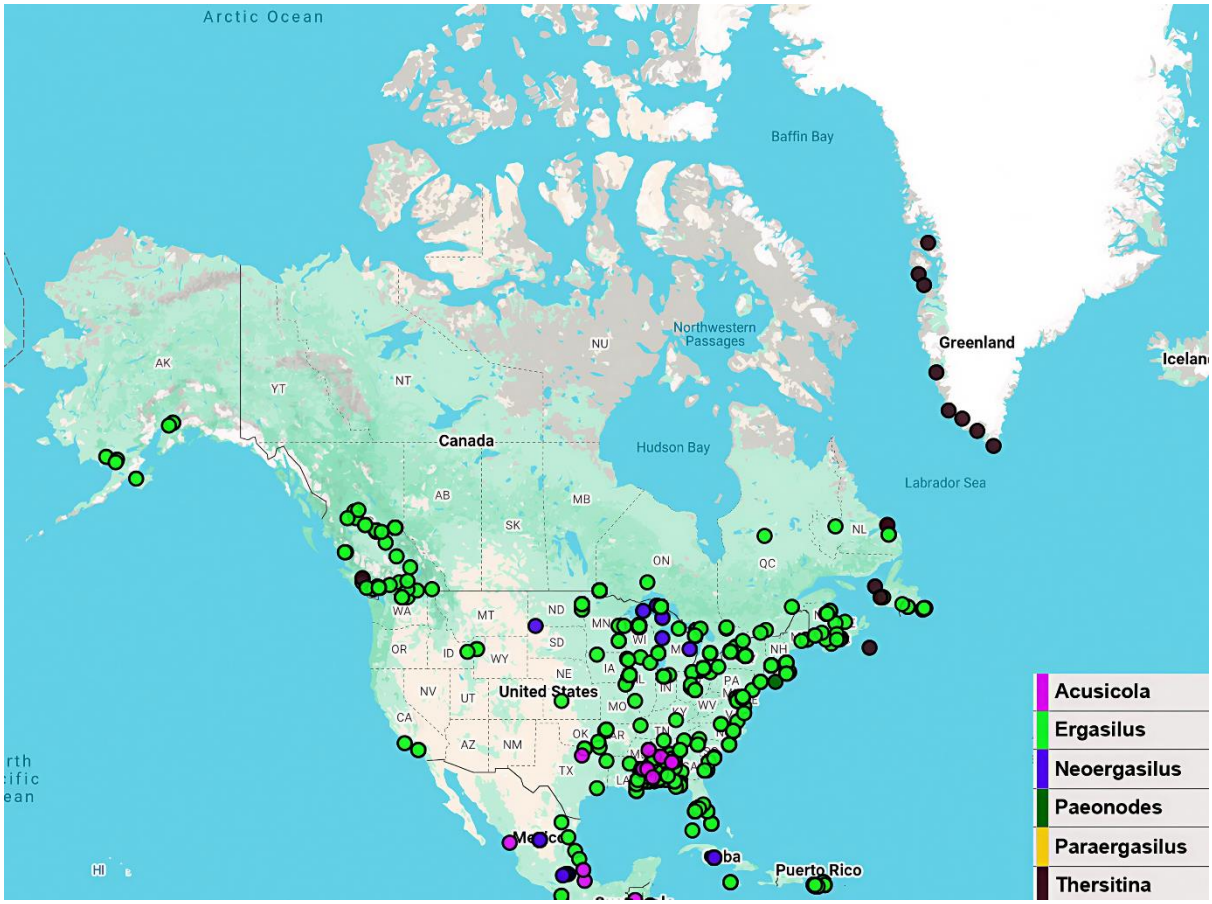


Figure 14. Locality records of Ergasilidae in the Nearctic region, colour-coded by genus.



Figure 15. Locality records of Lernaeidae in the Nearctic region, colour-coded by genus.

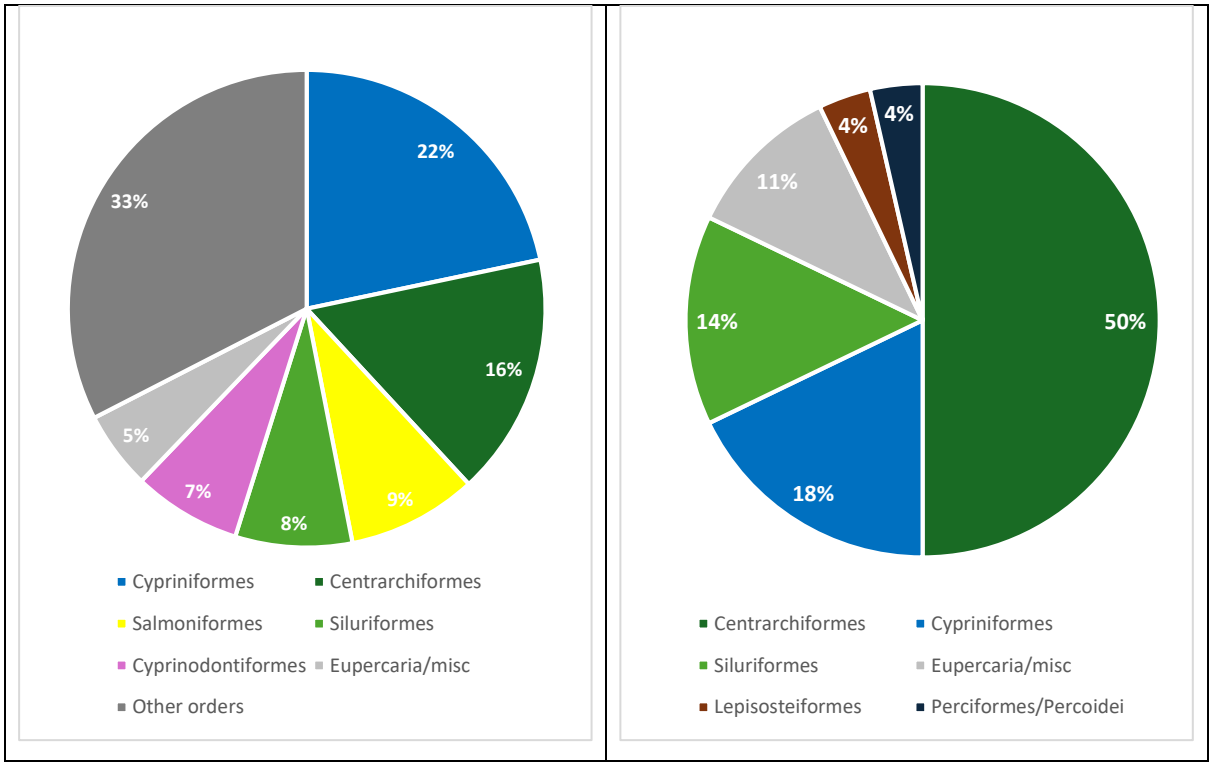


Figure 16. Relative representation of host orders in Nearctic ergasilid (a) and lernaeid (b) records; minor categories are aggregated as "other orders". Percentages expressed as proportions of total host records.

Australasian region

The Australasian region contains 20 valid ergasilid species belonging to 8 genera. Its fauna combines widespread Old World genera with a small number of regionally restricted lineages. The dominant genera are *Ergasilus* (7), *Dermoergasilus* (3) and *Paraergasilus* (3), with single species of *Neoergasilus* (1), *Paeonodes* (1) and *Mugilicola* (1), reflecting a mixture of marine, brackish and freshwater hosts distributed across continental Australia, New Guinea, New Zealand and adjacent islands (Fig. 17). The region also contains *Abergasilus* (1) and *Majalincola* (1), which represent two clearly endemic Australasian ergasilid lineages. Despite the high fish diversity of the region, ergasilid richness remains modest and shows limited generic expansion relative to the Neotropics and Oriental region. Lernaeidae are represented by only two species, both assigned to *Lernaea* (2), namely the cosmopolitan *L. cyprinacea* and *L. papuensis*, the latter endemic to Papua New Guinea (Fig. 18). No indigenous lernaeid genera occur in the region.

Host composition indicates that ergasilid occurrences in Australasia are dominated by hosts assigned to Eupercaria/Sparidae and Mugiliformes, followed by smaller contributions from Centrarchiformes, Anguilliformes, Siluriformes and Pleuronectiformes, followed by a substantial number of infrequently sampled taxa. Lernaeid records are narrowly distributed among Centrarchiformes, Osteoglossiformes, Galaxiiformes, Cypriniformes, Siluriformes and Cyprinodontiformes, most of them representing *Lernaea cyprinacea* (Fig. 19).

The regional parasitological record is historically sparse. Early scattered descriptions (Percival, 1937; Hewitt, 1969, 1978, 1979; Hine, 1978 were followed by broader parasitological surveys in eastern Australia during the 1980s and 1990s (Jones, 1981; Roubal, 1981, 1982, 1989, 1990, 1995; Byrnes, 1986; Byrnes & Rohde, 1992). Subsequent work has proceeded slowly and remains geographically uneven, with only a few new reports (El-Rashidy & Boxshall, 2001b; Tang & Kalman, 2008; Hassan *et al*., 2008). Large areas of northern and western Australia, New Guinea and adjacent island remain effectively unstudied. As a result, present host and parasite distributions almost certainly underestimate the true diversity of both families in the region.



Figure 17. Locality records of Ergasilidae in the Australasian region, colour-coded by genus. Points represent all confirmed published occurrences in Australia, Papua New Guinea and New Zealand.



Figure 18. Locality records of Lernaeidae in the Australasian region, colour-coded by genus. Points represent all confirmed published occurrences in Australia and Papua New Guinea.

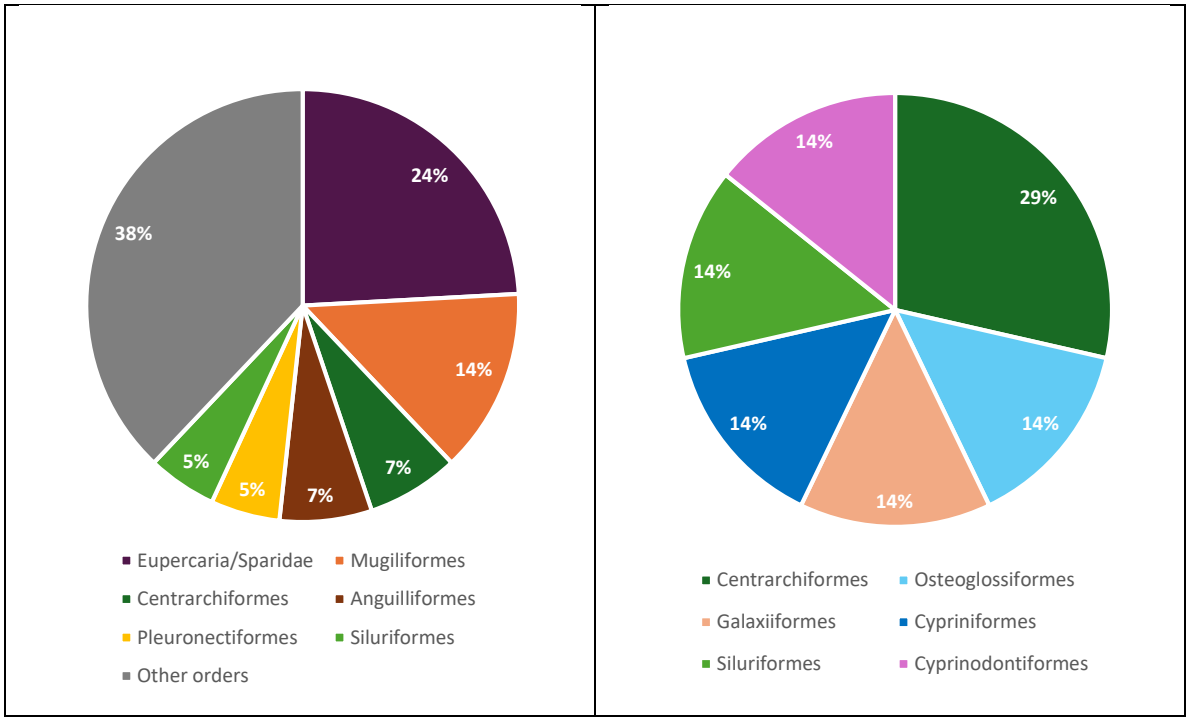


Figure 19. Relative representation of host orders in Australasian ergasilid (a) and lernaeid (b) records; minor categories are aggregated as "other orders". Percentages expressed as proportions of total host records.

Pacific Ocean Islands region

The Pacific Oceanic Islands contain only 2 valid ergasilid species belonging to 2 genera. These species represent isolated occurrences of *Ergasilus* (1) and *Paeonodes* (1) (Fig. 20). The reported ergasilid occurrences are *Ergasilus orientalis* in Tahiti and *Paeonodes subviridis* in Guam, both associated with Mugiliformes in marginal coastal habitats (Fig. 21). No genus is endemic to the Pacific islands, and the extremely low diversity probably corresponds with the limited freshwater habitats available on many islands and the absence of large, diverse lacustrine systems. There are no confirmed records of Lernaeidae in this region.

Taxonomic work in the Pacific islands has been extremely limited, consisting of a few isolated records associated with broader surveys of Indo-Pacific mugilids (El-Rashidy & Boxshall, 2001b, 2002). No freshwater parasitic copepod fauna has yet been documented from the vast majority of island groups, and most high islands have never been surveyed. The apparent absence of Lernaeidae is therefore best regarded as an artefact of incomplete sampling rather than true regional absence.

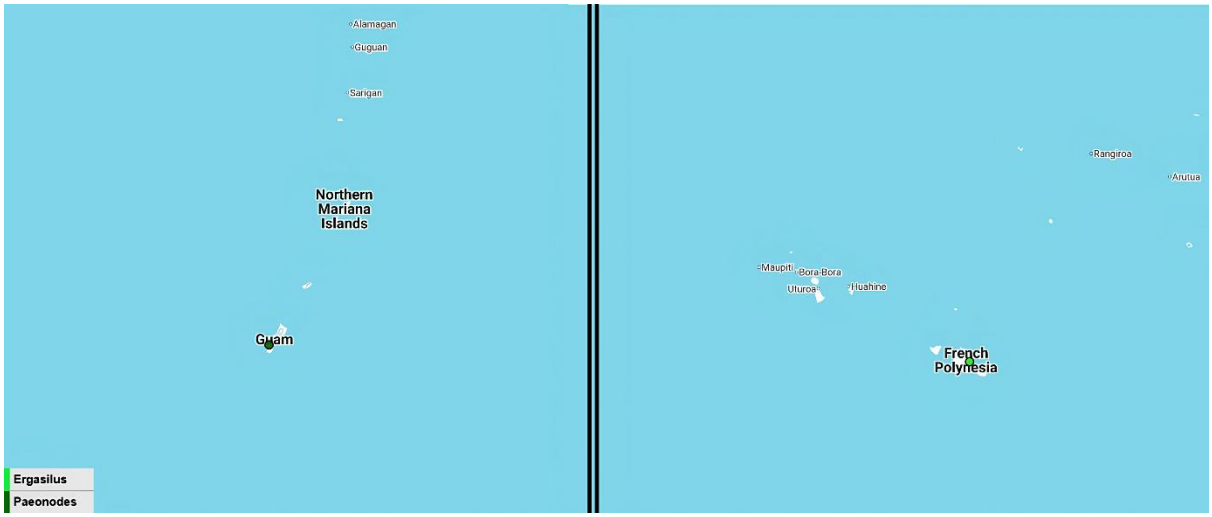


Figure 20. Locality records of Ergasilidae in the Pacific Ocean Islands region, colour-coded by genus. Points represent all confirmed published occurrences in Guam and French Polynesia.

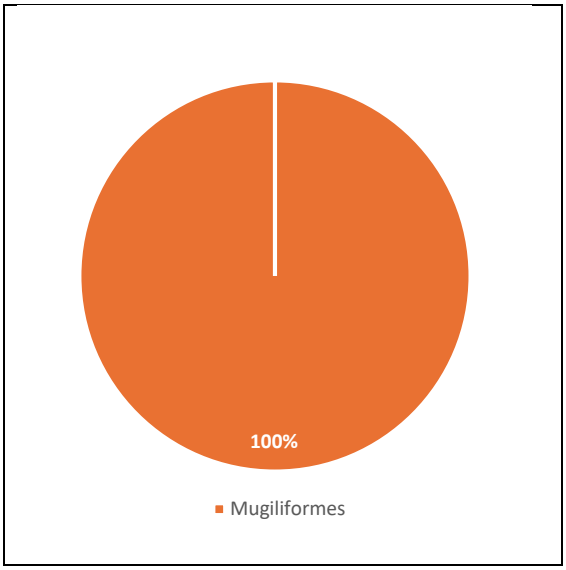


Figure 21. Relative representation of host orders in Pacific Ocean Islands ergasilid records; no lernaeids are present. Percentages expressed as proportions of total host records.

Antarctic region

The Antarctic region has no recorded species of Ergasilidae or Lernaeidae.

Invasive species: *Lernaea cyprinacea* and *Neoergasilus japonicus*

Anthropogenic translocation of freshwater fishes has profoundly altered the contemporary distribution of parasitic copepods, particularly within Ergasilidae and Lernaeidae. Among the taxa treated in this review, two species meet established criteria for invasive parasites by Kolar

& Lodge (2001) and require explicit separation from native biogeographical patterns: *Neoergasilus japonicus* and *Lernaea cyprinacea*.

Neoergasilus japonicus is native to East Asia and was originally described from cyprinid hosts in Taiwan (Harada, 1930) and assigned to *Ergasilus*, later transferred to *Neoergasilus* by Yin (1956). The species remained restricted to its native range until the mid-twentieth century. The earliest European records date to the 1960s from Hungary and Slovakia (Hanek, 1968; Pónyi & Molnár, 1969), most likely associated with ornamental and aquaculture fish imports from East Asia (Alekseev *et al*., 2021). Subsequent records document establishment in Cuba during the 1980s (Prieto *et al*., 1985) and continental North America during the 1990s (Hayden & Rogers, 1998; Suárez-Morales & Mercado-Salas, 2013). Since then, the species has expanded rapidly and is now widely distributed across Asia, Europe and the Americas, with confirmed records from multiple African countries indicating ongoing secondary spread (Nagasawa & Uyeno, 2012; Ondračková *et al*., 2019, 2025a). This species exhibits one of the widest host ranges known among ergasilids. Based on verified records compiled by Ondračková *et al*. (2025a) and updated from Míč *et al*. (2025), the species has been reported from at least 145 fish host species, spanning at least 15 orders and over 27 families. Its ability to switch readily from non-indigenous hosts to native fishes has facilitated rapid population establishment in invaded regions (Hudson & Bowen, 2002). Owing to its extensive host range, repeated transcontinental introductions and sustained population growth, *N. japonicus* is now recognised as an invasive parasitic copepod and has been prioritised for ecological risk assessment in several regions, including the North American Great Lakes (Bell *et al*., 2023). All confirmed country records of *N. japonicus* are synthesised in a dedicated species-level map (Fig. 22).

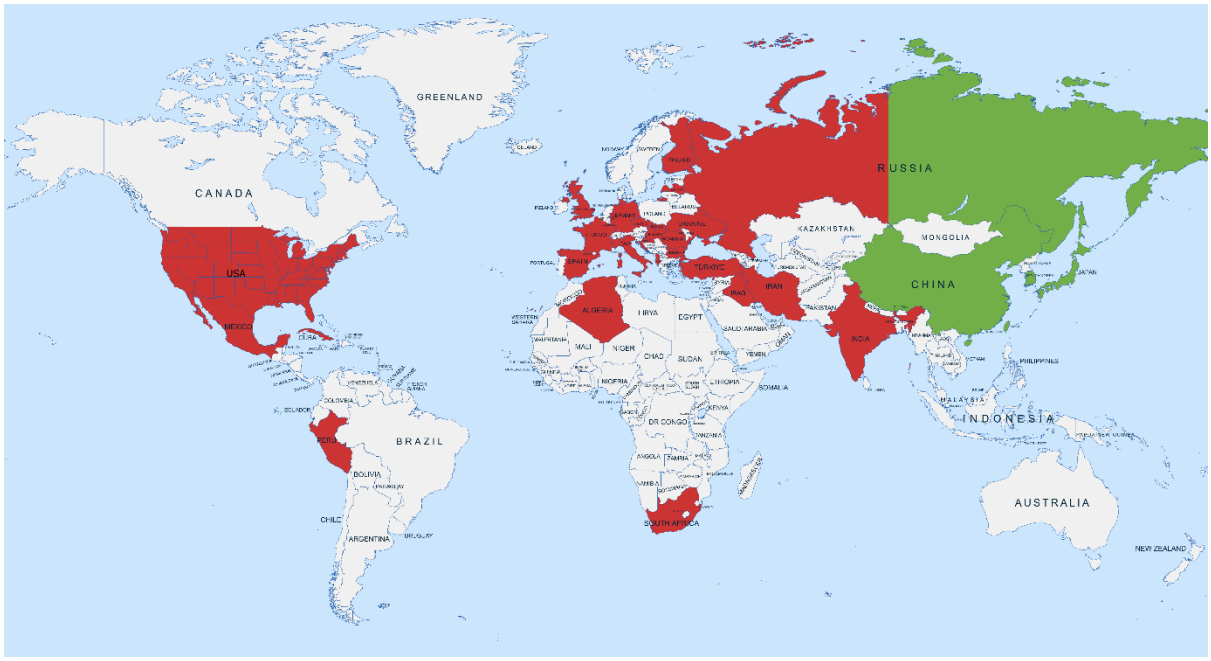


Fig. 22: Current reports of *N. japonicus* worldwide in its expected native (green) and non-native (red) range, Russia is denoted as both native and non-native range as the parasite naturally occurs in Far East Russia but has been introduced to the western part of the country; adapted from Ondračková *et al.* (2025a)

Lernaea cyprinacea represents an even more extreme example of invasion driven global dispersal. Although originally described from Europe, the species underwent rapid worldwide expansion during the twentieth century, closely following the global spread of cyprinid aquaculture and translocation of freshwater fishes (Harding, 1950; Kabata, 1979). It is now established on all continents except Antarctica and the Pacific Oceanic Islands. *Lernaea cyprinacea* possesses the widest host range documented for any freshwater parasitic copepod. Based on the present global synthesis, it has been recorded from more than 270 fish species, representing over 30 host orders and at least 80 families, and is also occasionally reported from amphibian hosts. Native fishes in invaded regions often exhibit higher susceptibility and pathology than co-evolved hosts (Welicky *et al.*, 2017; Waicheim *et al.*, 2019). The global distribution of *L. cyprinacea* has been further obscured by the high morphological variability of the adult female holdfast, which historically resulted in the description of numerous nominal species and subspecies based on minor shape differences (Leigh-Sharpe, 1925; Stunkard & Cable, 1931; Tidd, 1934; Yü, 1938; Hu, 1948; Gnanamuthu, 1951; Demaree, 1967). Later investigations produced experimental evidence when Poddubnaya (1973, 1978) reared larvae from a single female and showed that adults developed into multiple morphotypes historically interpreted as distinct species (*L. elegans*, *L. ctenopharyngodonis*, *L. quadrinucifera*), depending exclusively on host identity. Cytogenetic studies by Fratello & Sabatini (1972) revealed identical chromosome complements within morphologically divergent African and

European *Lernaea*, demonstrating that phenotype alone could not be used for secure taxonomy. Molecular analyses have shown that several of the nominal taxa do not represent distinct evolutionary lineages but fall within the variation of *L. cyprinacea*, supporting the interpretation of a single, widely invasive species rather than multiple regionally endemic forms (Hua *et al*., 2019). The taxonomic situation is further complicated by the absence of original type material for *L. cyprinacea* and by the extremely brief and outdated nature of the original description (Linnaeus, 1758), which predates modern standards of copepod taxonomy. As a result, comparative assessment of morphological variation among nominal *Lernaea* species is severely constrained. Many described taxa that closely resemble *L. cyprinacea* may in fact represent the same species, but the lack of type material and the absence of a stable morphological reference make reliable delimitation impossible. A comprehensive revision of *L. cyprinacea* sensu lato and of all morphologically similar species, integrating redescribed material from type or historically relevant localities with molecular data, is therefore required to establish relevant species boundaries.

Many published records of *L. cyprinacea* lack precise locality data and are reported only at national or regional scale. Because the sheer number and global spread of these records obscure regional patterns of native lernaeid diversity, the distribution of *L. cyprinacea* is treated separately and illustrated in an independent global map (Fig. 23).

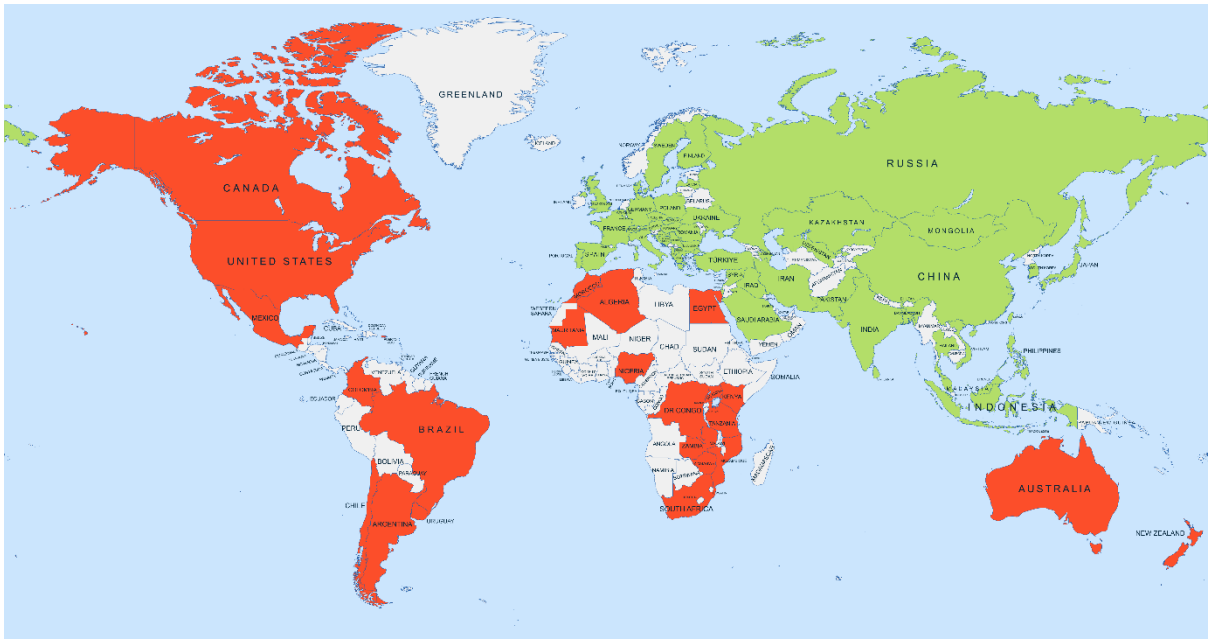


Fig. 23: Current reports of *L. cyprinacea* worldwide in its expected native (green) and non-native (red) range, only verifiable records are included

Host relationships and host specificity in Ergasilidae

Host spectrum

The distribution of host orders parasitised by Ergasilidae is markedly uneven (Fig. 24). Cypriniformes contain by far the largest number of parasitised species (261) and form the dominant component of the host spectrum, followed by Siluriformes (87), Cichliformes (84), Characiformes (76), Mugiliformes (38) and Cyprinodontiformes (33). In proportional terms, cypriniform fishes account for 28.8% of all host occurrences (Fig. 25), reflecting both their broad ecological range and their exceptional diversity in freshwater systems, as well as the long history of parasitological work on cyprinids and leuciscids. Siluriformes form the second most frequently parasitised group (roughly 10% of all host records).

Several additional freshwater orders, including Cichliformes, Characiformes, Mugiliformes, Centrarchiformes and Salmoniformes, show intermediate representation and each contributes between 5 and 8% of total records. A broad set of other teleost lineages is represented by few records individually; when pooled, these orders form a substantial "other" category that comprises approximately one quarter of all host occurrences, highlighting the wide phylogenetic reach of the family despite strong concentration on a few dominant orders.

At family level, Leuciscidae (100) and Cichlidae (84) represent the most frequently parasitised groups, followed by Cyprinidae (66), Mugilidae (38), Xenocyprididae (34), Gobionidae (26) and Salmonidae (23). Most remaining families contribute only a small number of records (Fig. 26).

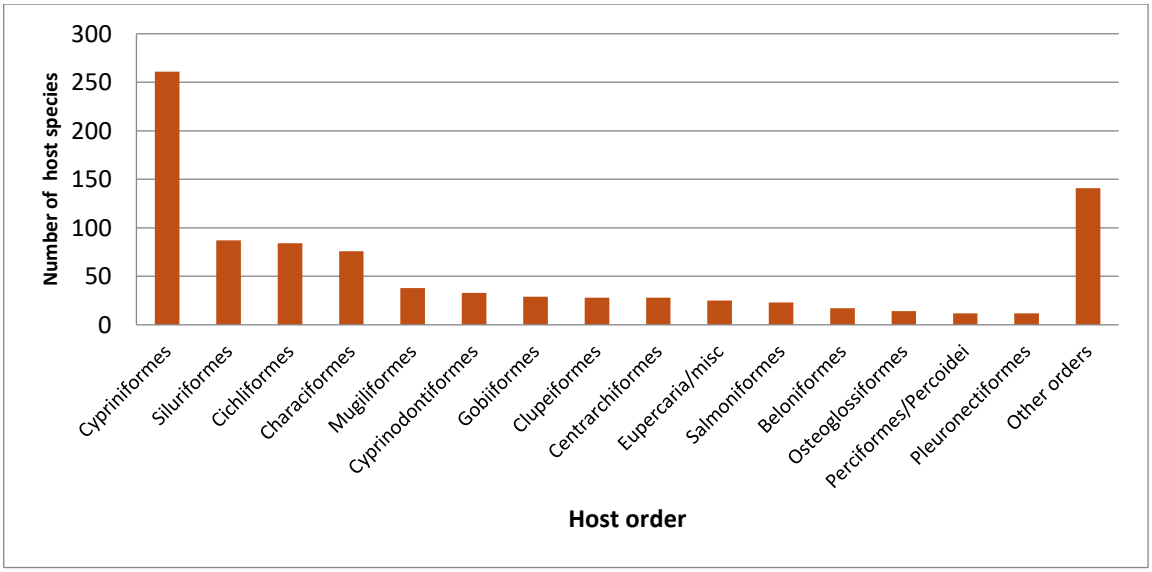


Fig. 24. Distribution of ergasilid parasite records across host orders.

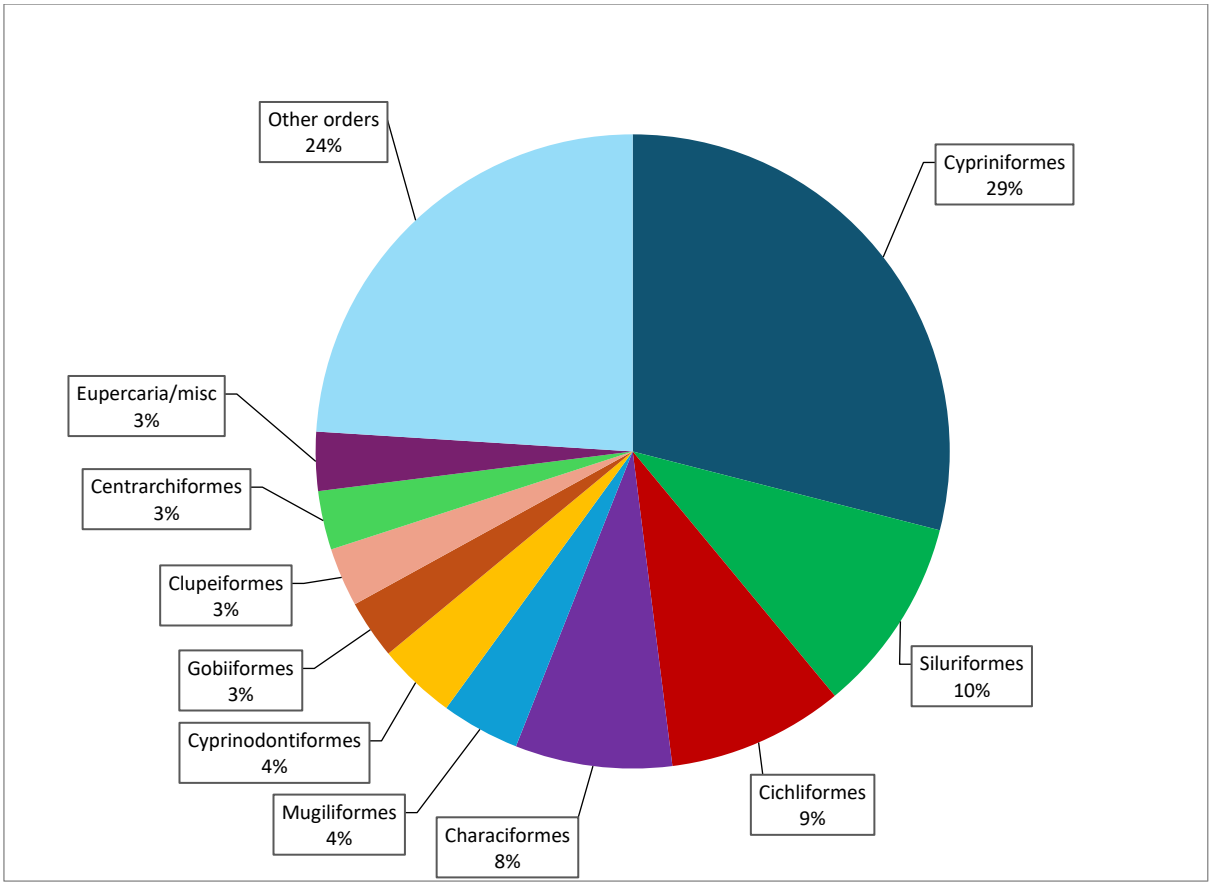


Fig. 25. Proportional representation of host orders parasitized by members of the Ergasilidae.

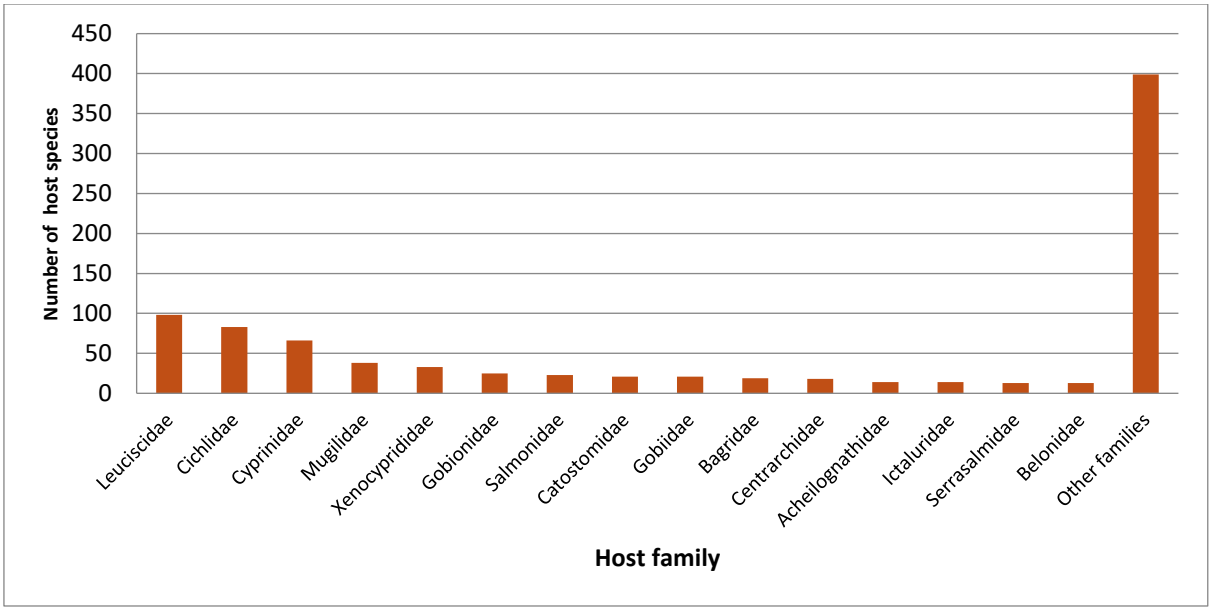


Fig. 26. Distribution of ergasilid parasite records across host families.

Ergasilid records are most frequently associated with a limited set of widely occurring fish species (Fig. 27). *Mugil cephalus* accounts for the highest number of parasite records (23), followed by *Cyprinus carpio* (18) and *Carassius auratus* (16). Additional cypriniform,

mugiliform and cichlid hosts dominating the upper distribution include *Planiliza subviridis* (13), *Ctenopharyngodon idella* (11), *Carassius carassius* (11), *Planiliza abu* (11), *Coptodon zillii* (11), *Carasobarbus luteus* (10), *Rutilus rutilus* (8), *Zacco platypus* (8), *Leuciscus vorax* (8) and *Osteomugil cunnesius* (8). Further notable contributions arise from *Gasterosteus aculeatus* (9) and *Micropterus salmoides* (9). All remaining host species are associated with eight or fewer ergasilid species.

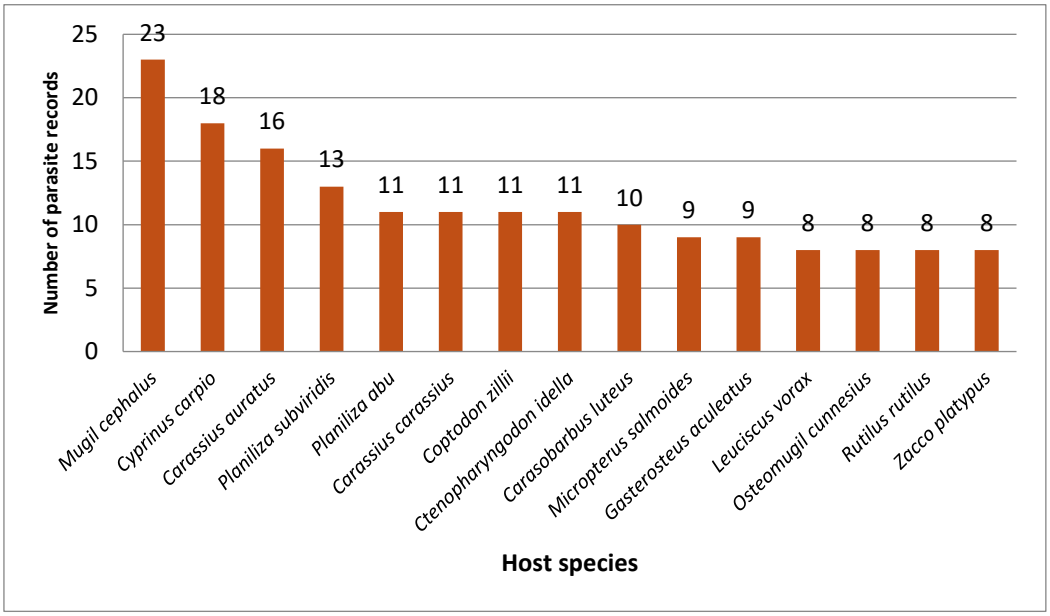


Fig. 27. Host species with the highest numbers of recorded Ergasilidae associations (top 15). Values represent unique host–parasite species records per host species.

Host specificity patterns

Most ergasilid species are known from a single host, and the number of species associated with multiple hosts declines steadily with increasing host range (Fig. 28). More than one hundred species occur on only one host, whereas progressively fewer are associated with 2–3 hosts or 4–10 hosts. Only a small subset is known from more than ten host species. This pattern is likely influenced by the large proportion of species known only from their original descriptions or from very few subsequent records, which limits inferences about their true host range.

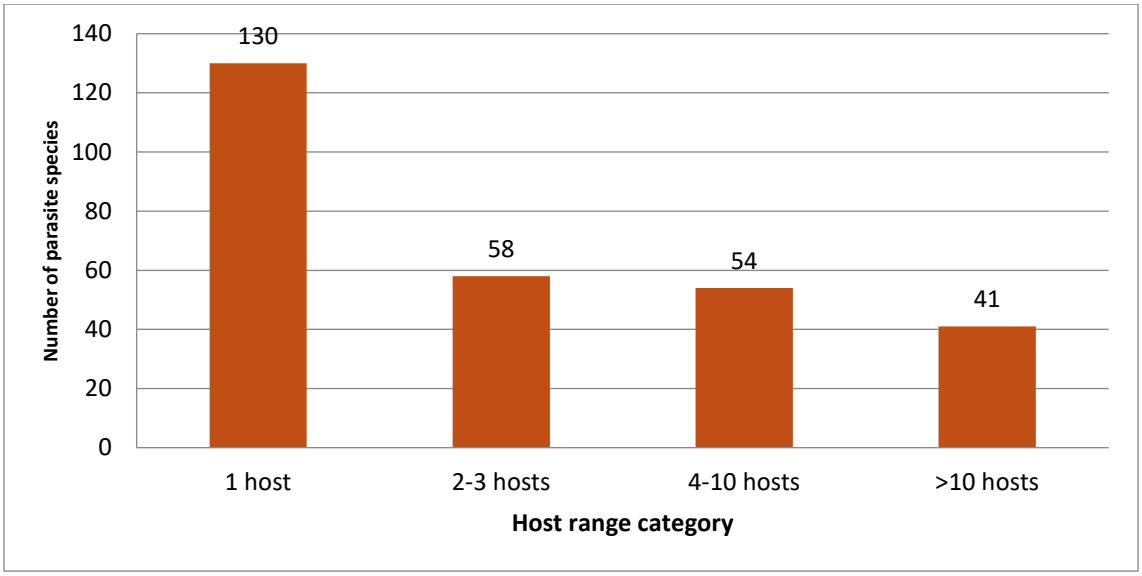


Fig. 28. Distribution of host range categories among ergasilid species.

At the generic level, narrow host associations predominate. Most genera contain species with very restricted host use, whereas wide host ranges are largely confined to *Ergasilus* and, to a lesser extent, *Neoergasilus* (the latter mainly due to the invasive *Neoergasilus japonicus*) (Fig. 29). The widest host ranges are restricted to a few widely distributed species: *N. japonicus* has the largest number of recorded hosts (145), followed by *Ergasilus sieboldi* (108), *E. lizae* (70), *E. briani* (57) and *E. caeruleus* (42). Additional broadly distributed species include *Paraergasilus longidigitus* (33), *E. versicolor* (31), *E. rostralis* (26), *E. mosulensis* (25) and *E. nerkae* (25).

At generic scale, *Ergasilus* forms the dominant component of the dataset with at least 665 recorded host species, followed by *Neoergasilus* with 170 hosts and *Paraergasilus* with 75 hosts, whereas all remaining genera are associated with only very small numbers of recorded hosts and are often known from single or few records (Fig. 30).

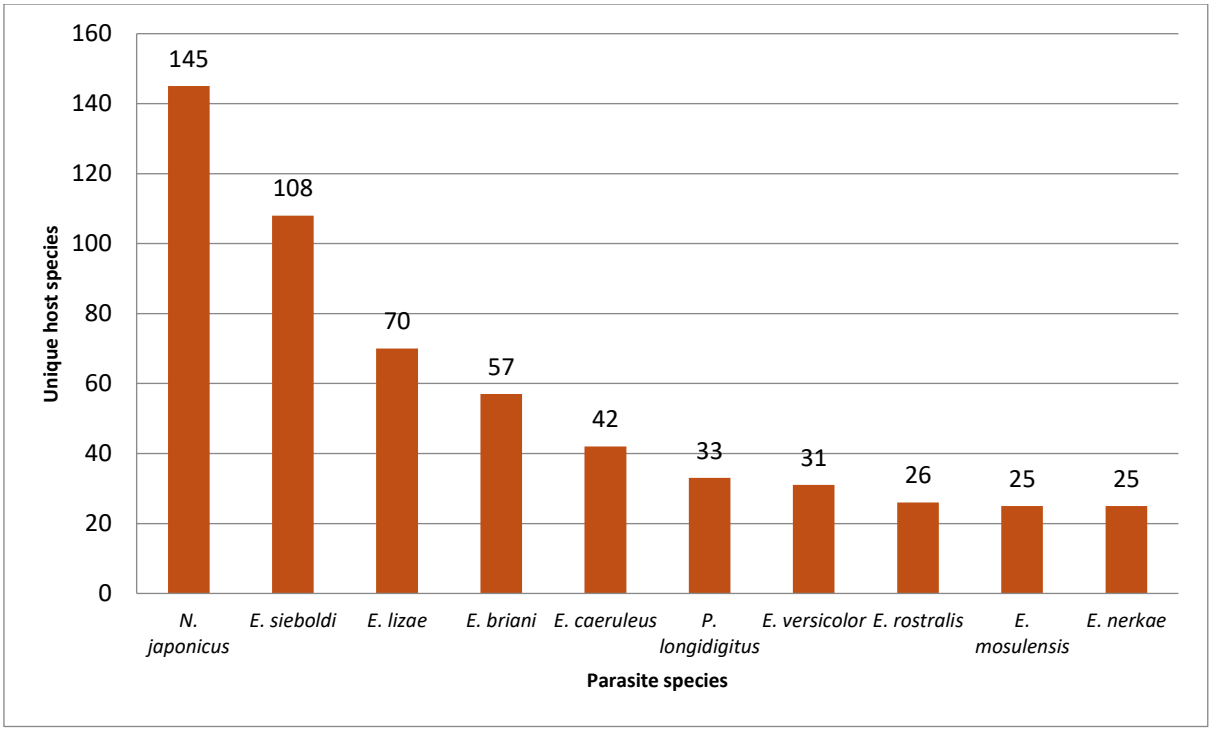


Fig. 29. The ten ergasilid species with the widest recorded host range.

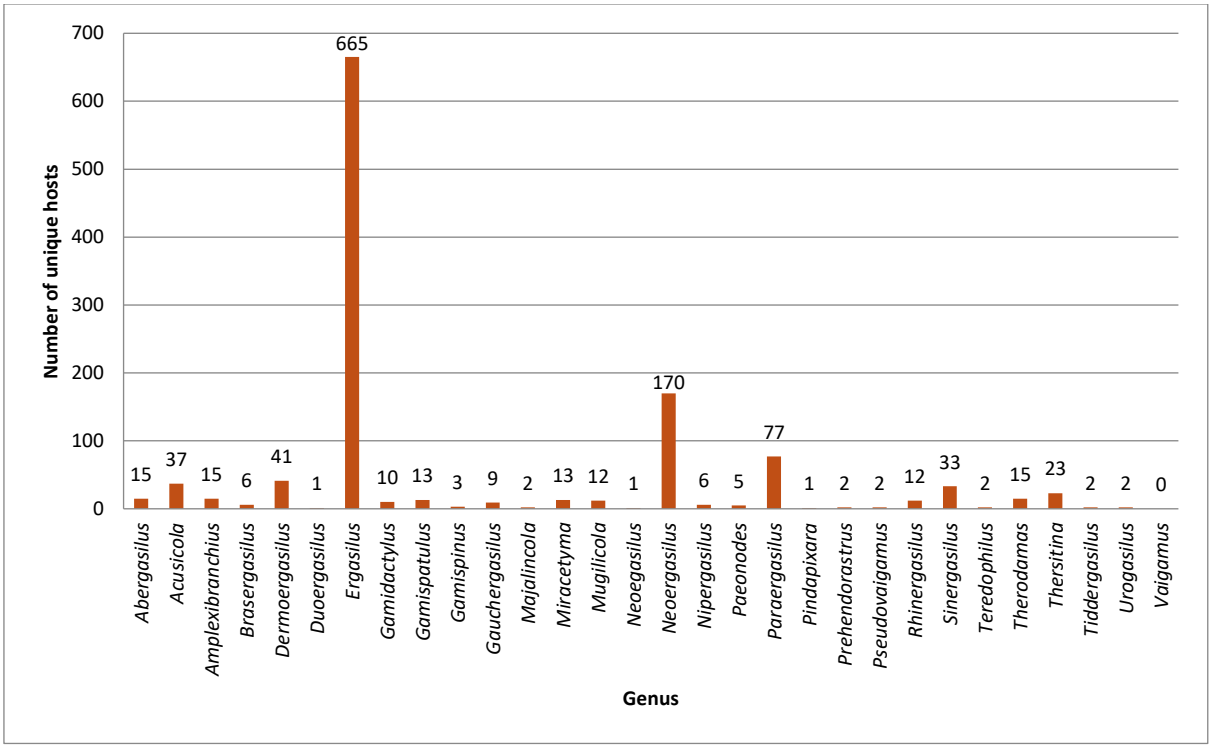


Fig. 30.: Number of unique host species recorded for each genus of Ergasilidae (*Vaigamus* has been recorded only from plankton material).

Host relationships and host specificity in Lernaeidae

Host spectrum

The distribution of host orders parasitised by Lernaeidae is likewise highly uneven. Cypriniformes constitute the dominant component of the host spectrum, with at least 260 distinct host species and 49% of all host occurrences. Cichliformes represent the second most frequently parasitised order, with 67 species (13%). Together, these two orders account for more than 62% of all lernaeid host occurrences (Fig. 31).

Several primarily freshwater orders exhibit intermediate representation. Siluriformes contribute 39 species (7%), Characiformes 29 species (5%) and Perciformes 25 species (5%). Additional contributions are made by Cyprinodontiformes (19), Anabantiformes (12), Osteoglossiformes (12), Centrarchiformes (10) and Gobiiformes (9). A wide array of further teleost orders (including Polypteriformes, Mugiliformes, Salmoniformes, Esociformes, Acipenseriformes, Scorpaeniformes and others) are represented by few records each but collectively emphasise the broad phylogenetic scope of the family (Fig. 32).

At family level, Cyprinidae (148) are the principal hosts, followed by Cichlidae (67) and Leuciscidae (66). Additional frequently parasitised families include Centrarchidae (17), Xenocyprididae (16), Bagridae (11), Catostomidae (10) and Poeciliidae (10). Most remaining families contribute only a small number of records and form a long tail of infrequently infected taxa (Fig. 33).

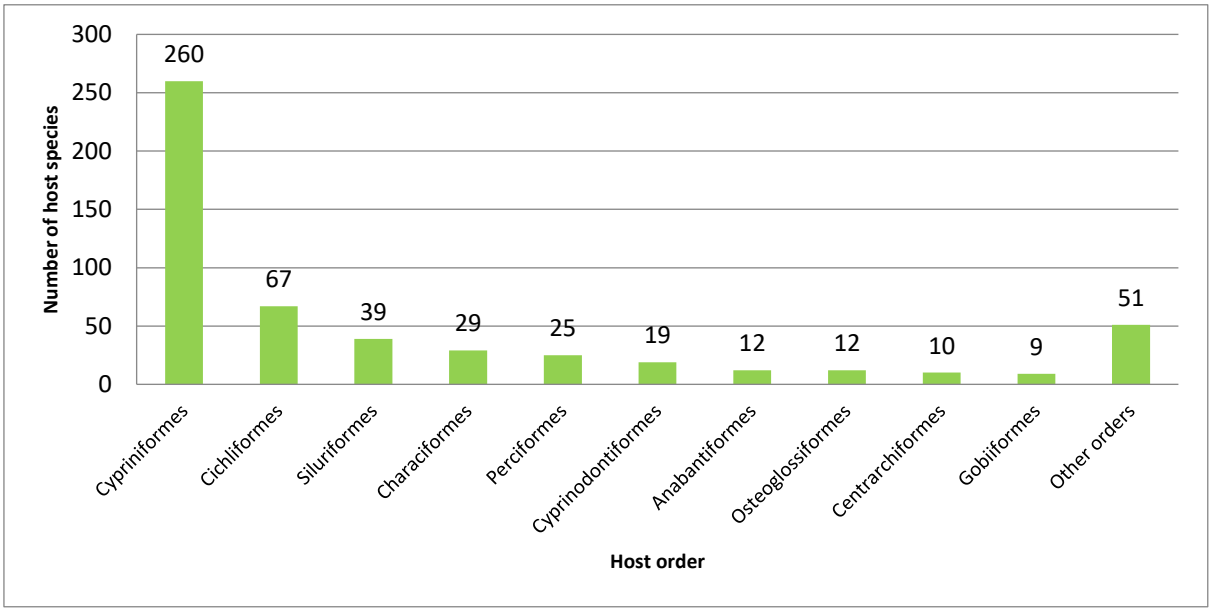


Fig. 31. Distribution of lernaeid parasite records across host orders. The ten most represented orders are shown; all remaining orders are combined under “Other orders”.

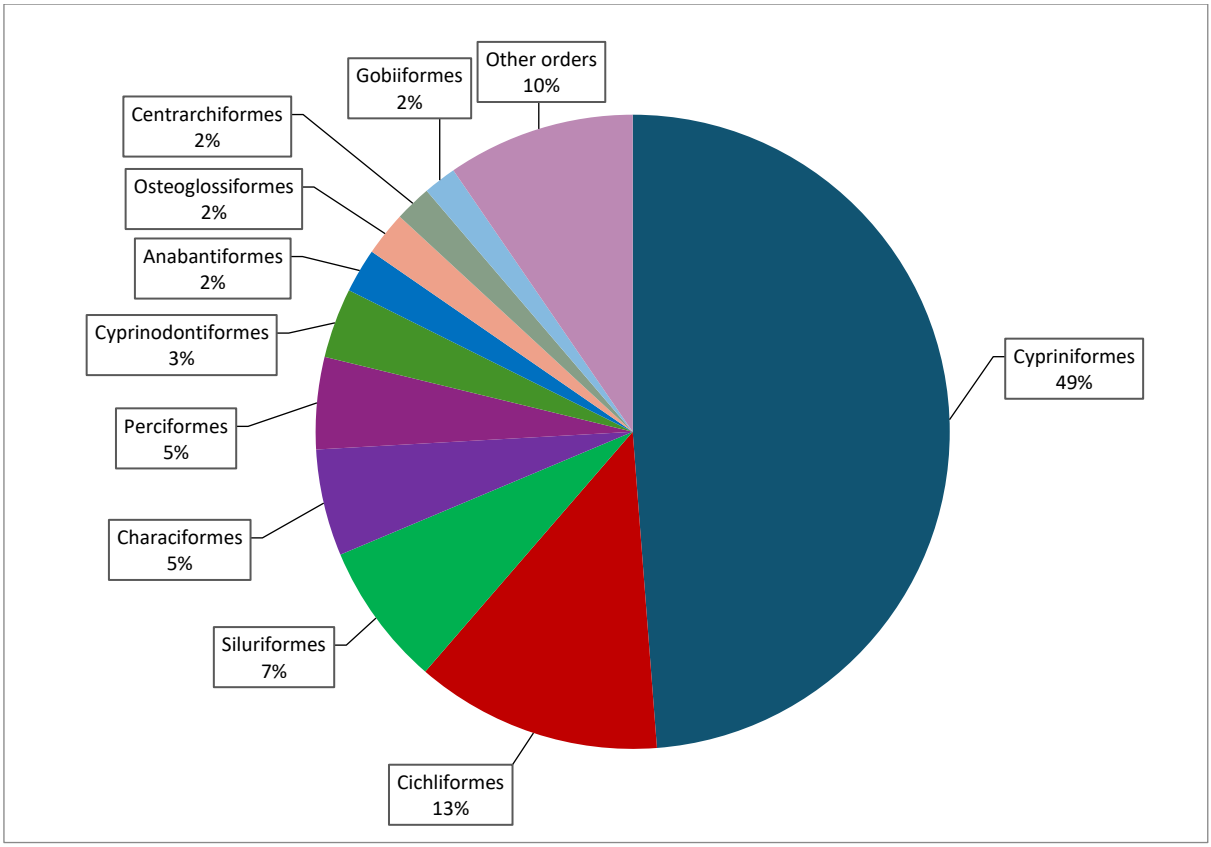


Fig. 32. Proportional representation of host orders parasitized by members of the Lernaeidae.

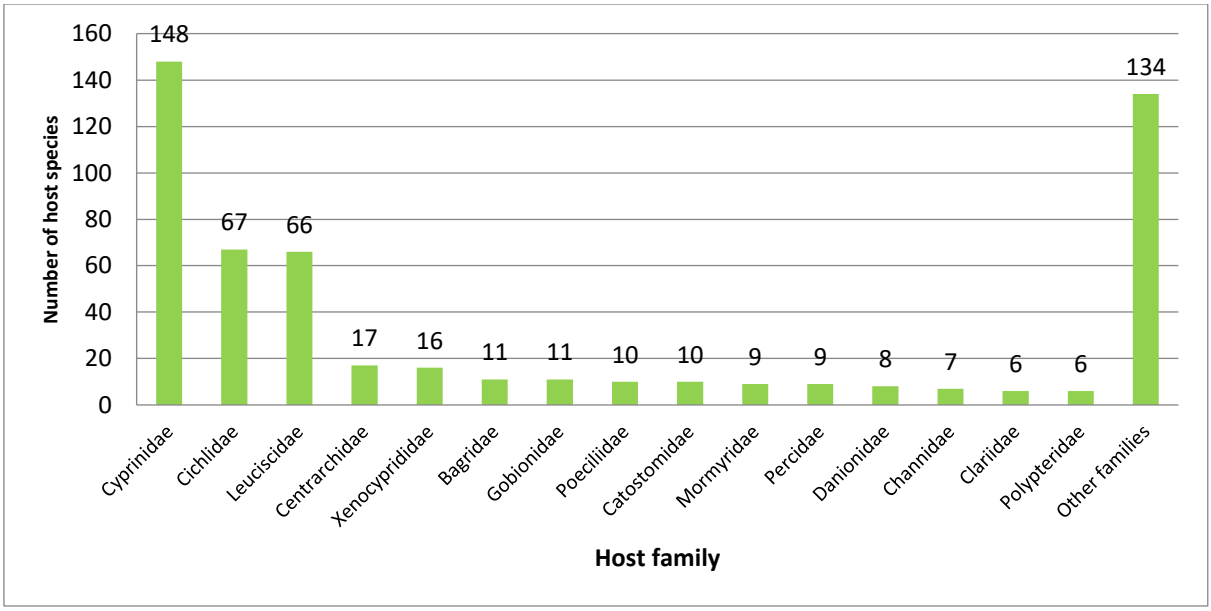


Fig. 33. Distribution of lernaeid parasite records across host families. The ten most represented orders are shown; all remaining orders are combined under "Other orders".

Lernaeid records are concentrated in a set of widely distributed freshwater hosts (Fig. 34). *Labeo catla* and *Hypophthalmichthys molitrix* exhibit the highest numbers of records and are each parasitised by 8 different lernaeid species, followed by *Cyprinus carpio* (7). Several

additional cypriniform, cichliform and anabantiform hosts follow, including *Labeo rohita* (6), *Oreochromis niloticus* (6), *Carasobarbus luteus* (5) and *Channa punctata* (5). Similar frequencies are documented for *Coptodon zillii* (5) and *Channa striata* (4), as well as *Notopterus notopterus*, *Barbonymus gonionotus*, *Lepomis gibbosus*, *Lepomis macrochirus*, *Leuciscus vorax* and *Ctenopharyngodon idella*, each contributing 4 records. All remaining host species are represented by fewer than four lernaeid species.

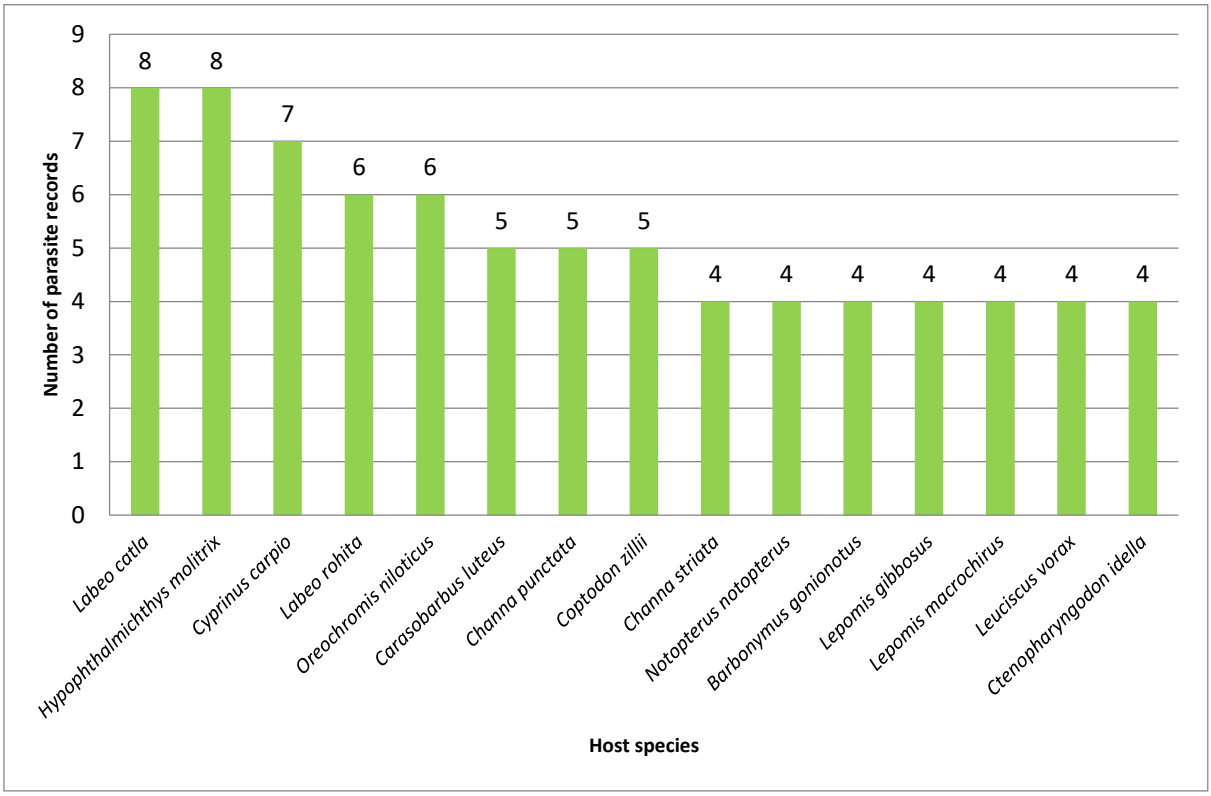


Fig. 34. Host species with the highest numbers of recorded Lernaeidae associations (top 15). Values represent unique host–parasite species records per host species.

Host specificity patterns

Most lernaeid species exhibit a narrow host range, and the majority (72 species) are recorded from only a single host (Fig. 35). Considerably fewer species are known from 2–3 hosts (23 species) or 4–10 hosts (23 species), and only a small subset (8 species) is associated with more than ten host species. As in Ergasilidae, this pattern almost certainly reflects, in part, the high proportion of species known only from one or few records, rather than strict host specificity.

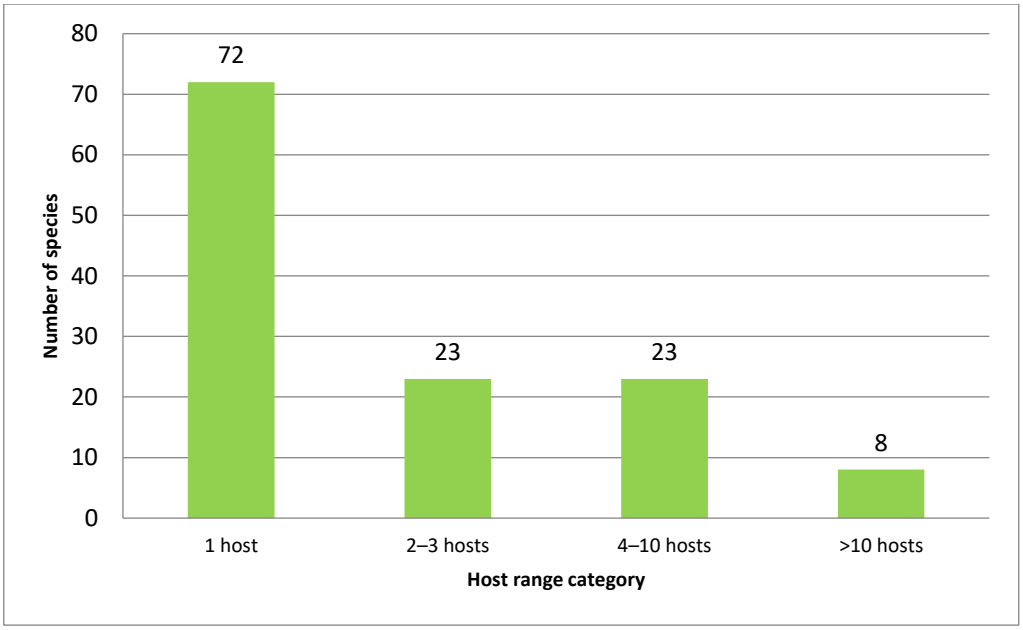


Fig. 35. Distribution of host range categories among lernaeid species.

The distribution of broad host generalists is concentrated in a few widely distributed species (Fig. 36). *Lernaea cyprinacea* exhibits the widest recorded host range by a very large margin, with over 270 host species, making it the most generalist member of the family by far. Substantially narrower but still broad ranges are displayed by *Lamproglena pulchella*, which is known from slightly more than 50 hosts, and by *Lamproglena monodi*, recorded from around 40 hosts. Several additional species show intermediate generalism, including *Lernaea barnimiana* (25), *Lernaea lophiara* (20), and *Lamproglena orientalis* (15). The remaining widespread generalists each parasitize between 10 and 15 host species and include *Lernaea cruciate* (12), *Pseudolamproglena annulata* (11), *Lernaea hardingi* (10), and *Lamproglena compacta* (10). Other species parasitize less than 10 hosts.

At the generic scale, host-use patterns remain highly skewed (Fig. 37). Only two genera contain species with exceptionally broad host associations. *Lernaea* is the dominant genus, with more than 360 unique host species, followed by *Lamproglena*, which collectively parasitizes around 180 host species. At the same time, these are by far the most speciose genera of the family. All remaining genera exhibit lower numbers of host ranges, each associated with fewer than 20 host species, and most represented by only one or a few documented records

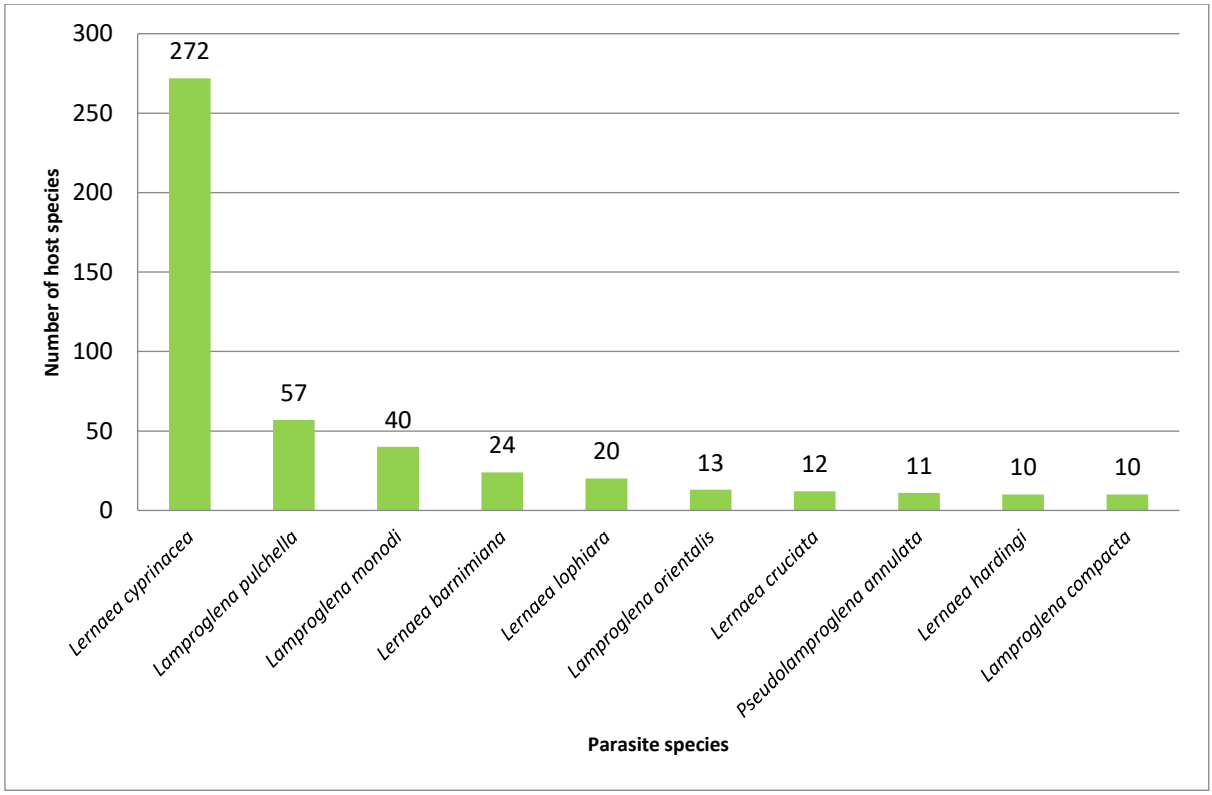


Fig. 36. The ten lernaeid species with the widest recorded host range.

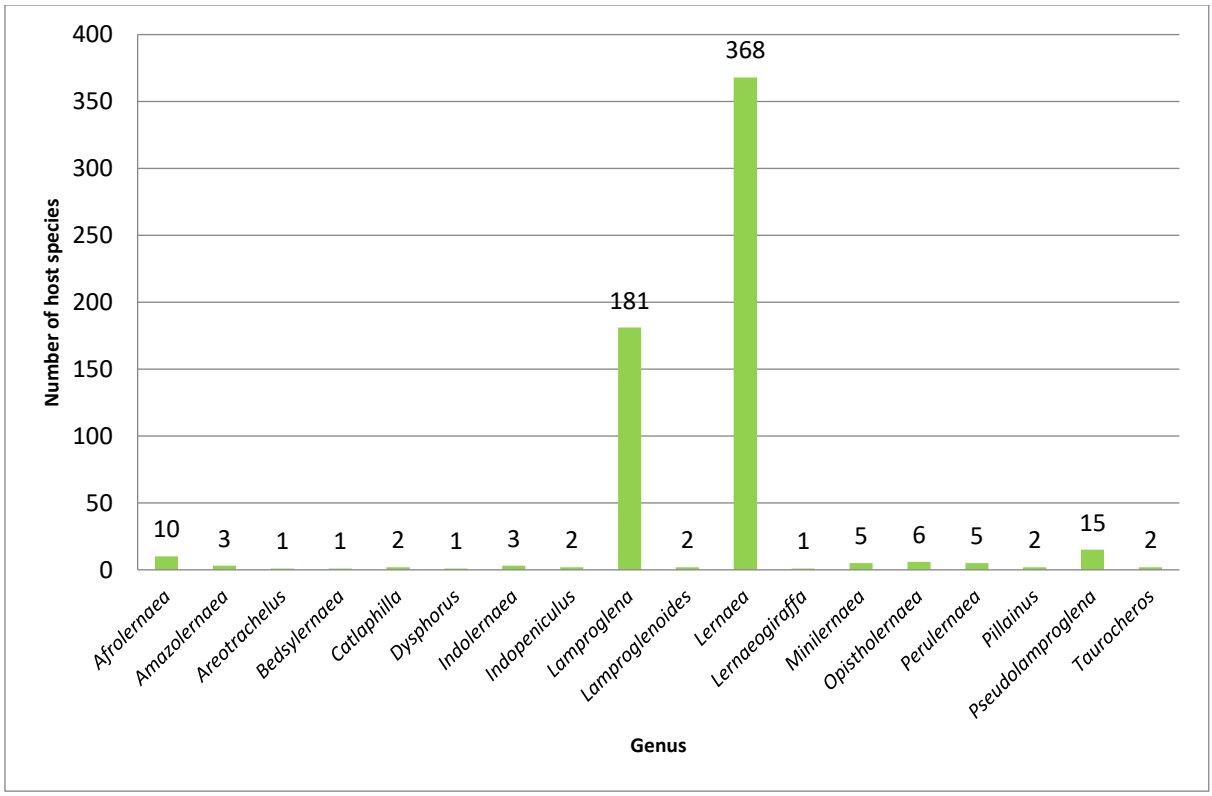


Fig. 37.: Number of unique host species recorded for each genus of Lernaeidae

Taxonomic adjustments

Several taxonomic decisions were necessary to standardise the global checklist.

***Dermoergasilus kabatai* (Thomas, 1994) comb. nov.**

Ergasilus kabatai Thomas, 1994 was described from adult females collected on the gills of *Mugil cephalus* from the Kerala coast of India, with the holotype deposited in the Indian Museum, Calcutta (Fig. 38). Although originally assigned to *Ergasilus*, the description and illustrations emphasise a suite of morphological characters diagnostic for *Dermoergasilus* Ho & Do, 1982, including a conspicuously inflated antenna with the second to fourth segments enclosed within a wrinkled sheath, a digitiform process associated with the caudal rami, and cephalothoracic subdivision consistent with the generic diagnosis. Thomas (1994) noted similarity to *E. coleus* and *E. semicoleus*, both later transferred to *Dermoergasilus* on the basis of identical antennal morphology. Accordingly, *Ergasilus kabatai* Thomas, 1994 is here transferred to *Dermoergasilus* as *Dermoergasilus kabatai* (Thomas, 1994) comb. nov.

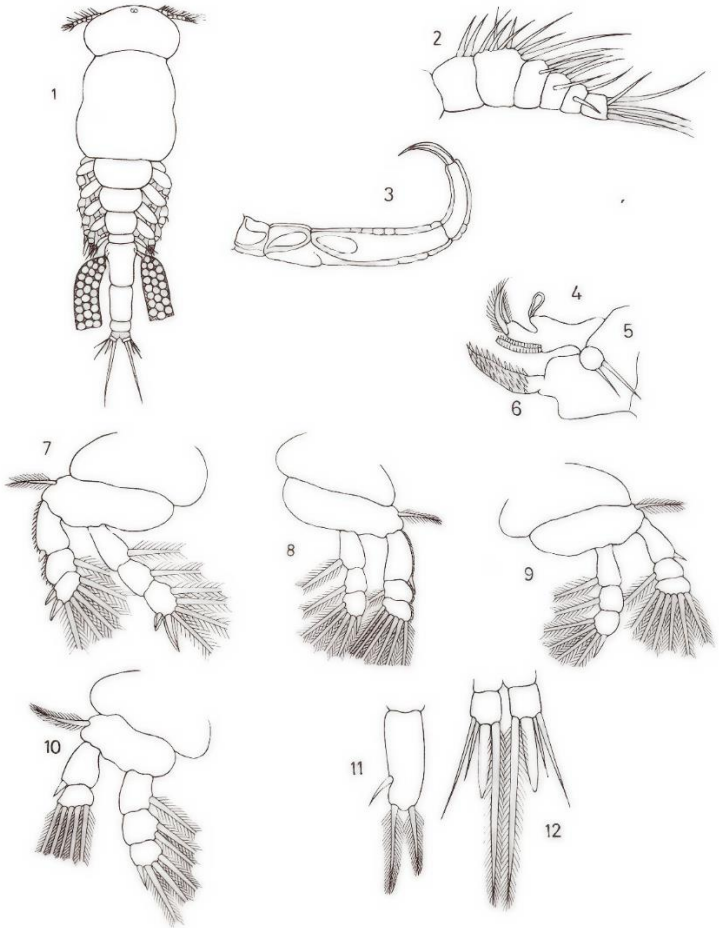


Fig 38. *Dermoergasilus kabatai* (Thomas, 1994) comb. nov., adult female. (1) habitus, dorsal; (2) antennule; (3) antenna; (4) mandible; (5) maxillule; (6) maxilla; (7) Leg 1; (8) Leg 2; (9) Leg 3; (10) Leg 4; (11) Leg 5; (12) caudal rami with digitiform process (adapted from Thomas, 1994).

Neoergasilus spinipes (Byrnes, 1986) comb. nov.

Ergasilus spinipes Byrnes, 1986 was described from adult females collected on the gills of *Acanthopagrus berda* in Queensland, Australia, with the holotype and paratype deposited in the Australian Museum (Fig. 39). Although originally placed in *Ergasilus*, the morphology illustrated by Byrnes (1986) conforms to the diagnostic character set of *Neoergasilus* Yin, 1956. The antenna is robust and subchelate, bearing a strongly curved claw with associated sensillar processes, leg 1 exhibits a conspicuous subtriangular exopodal process, and the genital complex bears a prominent ventral articulating spine, all characters typical of *Neoergasilus* and absent from valid representatives of *Ergasilus*. Kazachenko (2001) erected *Byrnesius* for this species, but this genus was subsequently synonymised with *Neoergasilus* by Boxshall & Halsey (2004). Despite this, the species has continued to appear under its original combination in later literature. The morphology of *E. spinipes* is distinct from that of the widespread invasive *N. japonicus* and from all other congeners. Accordingly, *Ergasilus spinipes* Byrnes, 1986 is here transferred to *Neoergasilus* as *Neoergasilus spinipes* (Byrnes, 1986) comb. nov.

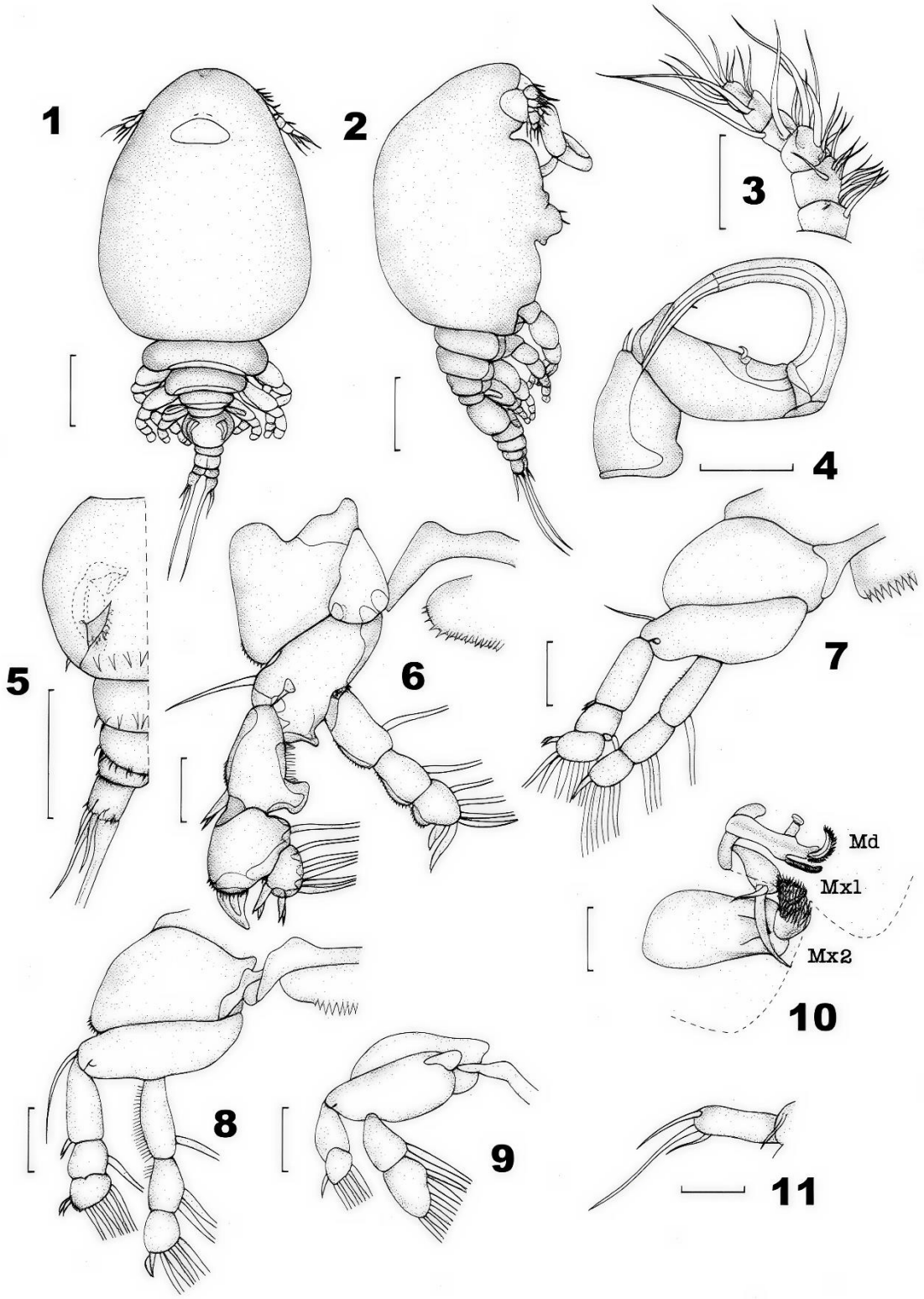


Fig 39. *Neoergasilus spinipes* (Byrnes, 1986) comb. nov., adult female. (1) habitus, dorsal; (2) habitus, lateral; (3) antennule, ventral; (4) antenna, ventral; (5) urosome, ventral; (6) Leg 1, ventral; (7) Leg 2, ventral; (8) Leg 3, ventral; (9) Leg 4, ventral; (10) mouthparts, ventral; (11) Leg 5, ventral; (adapted from Byrnes, 1986).

Ergasilus brevimanus Sars, 1909 *nomen dubium*

Sars (1909) described *Ergasilus brevimanus* from material collected in Lake Tanganyika. The taxon has long been considered problematic, and several authors have suggested that the original specimens were immature and unsuitable for reliable diagnosis (Fryer, 1968; Oldewage & van As, 1988). Direct examination of the type material preserved in the Natural History Museum, London confirms that all specimens represent juvenile stages lacking the adult morphological characters required for confident identification. Accordingly, *Ergasilus brevimanus* Sars, 1909 is regarded as *nomen dubium*.

Lernaea kuangi nom. nov.

Lernaea minuta Kuang, in Kuang & Qian, 1983 was described from freshwater fishes in China. However, the specific epithet *minuta* is preoccupied by *Lernaea minuta* T. Scott, 1900, currently placed in *Lernaeocera*. This homonymy is objective and permanent under the Code, irrespective of subsequent generic reassignment of Scott's species. The problem was recognised by Kularatne *et al.* (1994), who documented outbreaks of the same taxon in Malaysian aquaculture and noted explicitly that Kuang's name was unavailable, but no replacement name was proposed at that time, presumably in anticipation of a subsequent correction by the original author. No such action has been taken in the intervening decades, and the junior homonym has continued to appear in the literature.

As the taxon described by Kuang is morphologically distinct and its identity is not in doubt, the nomenclatural instability arises solely from homonymy rather than taxonomic uncertainty. To stabilise usage and remove the homonymy, the replacement name *Lernaea kuangi* nom. nov. is here proposed for *Lernaea minuta* Kuang, in Kuang & Qian, 1983.

Etymology. The replacement epithet is formed in honour of P. R. Kuang, who described numerous Chinese representatives of Lernaeidae and related parasitic copepods.

Molecular data and phylogenetic progress in Ergasilidae and Lernaeidae

Molecular sequencing of ergasilid and lernaeid copepods began relatively late compared with other parasitic crustacean groups. Early studies in the 1990s focused almost exclusively on cladistic analyses based on morphology (Amado *et al*., 1995; Ho, 1998), and DNA-based approaches did not enter the literature until the early 2000s. The first analyses involving ergasilid taxa were produced by Kim & Kim (2000), who examined partial 18S rDNA to assess

relationships among poecilostome families. Their results placed Ergasilidae within a clade comprising Lichomolgidae and Chondracanthidae, thereby establishing the first molecular framework for the group but without resolving internal relationships.

The first study to address phylogenetic structure within Ergasilidae was carried out by Song *et al.* (2008), who analysed partial 18S and 28S rDNA from *Sinergasilus*, *Paraergasilus*, *Ergasilus* (including material formerly assigned to *Pseudergasilus*), and several species of *Lamproglena* collected in China. All analytical methods employed (neighbour-joining, maximum parsimony, maximum likelihood and Bayesian inference) recovered *Sinergasilus* and *Paraergasilus* as monophyletic. In contrast, *Ergasilus* did not form a cohesive lineage and appeared polyphyletic, a result that directly corroborated earlier cladistic hypotheses based on morphological characters (Amado *et al*., 1995; El-Rashidy, 1999). Subsequent studies expanded taxon sampling but remained geographically uneven. In the Neotropics, Santacruz *et al.* (2020) provided the first molecular data for *Acusicola margulisae* from Central America, showing that it formed a distinct lineage sister to several ergasilid genera. In Brazil, additional analyses of related taxa confirmed the distinctiveness of multiple Amazonian lineages, in agreement with earlier morphological interpretations (Oliveira *et al*., 2021; Waicheim *et al*., 2021). In the Palaearctic, Kvach *et al.* (2021) presented the first sequences for *Ergasilus sieboldi* and *Paraergasilus longidigitus*, confirming the monophyly of *Paraergasilus*. African material entered the literature only recently, with sequences from newly described species from Lake Tanganyika (Míč *et al*., 2023), from *E. mirabilis* in southern Africa (Fikiye *et al*., 2023), from *E. kandti* (Jansen *et al*., 2025), from two marine *Ergasilus* species (van der Spuy et al., 2024) and from *Neoergasilus africanus* (Fikiye *et al*., 2024). New sequences for *Dermoergasilus* from Madagascar (Míč *et a*l., 2024) and *Rhinergasilus* from Brazil (Narciso *et al*., 2025), together with additional *Ergasilus* species from the Mediterranean and Middle East (Míč *et al*., 2025), further broaden generic coverage.

Work on the Lernaeidae has developed in parallel and initially concentrated on *Lernaea*. Hua *et al.* (2019) noted that several nominal species (*L. cruciate*, *L. ctenopharyngodontis* and *L. polymorpha*) may not represent distinct lineages and are conspecific with *L. cyprinacea*. Broader sampling of *Lamproglena* from African hosts demonstrated structure consistent with geographic origin (Dos Santos *et al*., 2023). Recent analyses added sequences for Palaearctic *Lamproglena pulchella* and first data for genus *Pseudolamproglena* (Míč *et al*., 2025). The invasive species *Lernaea cyprinacea* and *Neoergasilus japonicus* have now been sequenced repeatedly from multiple continents and represent the best-covered members of the families

(e.g. Stavrescu-Bedivan *et al*., 2014; Su *et al*., 2016; Ondračková *et al*., 2019; Kvach *et al*., 2021; Prastowo *et al*., 2023). Available sequences for both families are provided in Table 3.

Three markers dominate current work: partial 18S and 28S rDNA and mitochondrial COI. The 18S gene provides phylogenetic importance at family and genus levels but exhibits very limited variability among closely related species and rarely resolves congeneric taxa (Taniguchi *et al*., 2004; Tang *et al*., 2012). The 28S gene offers greater resolution and its diagnostic value increases substantially when interpreted in parallel with morphological characters (Morales-Serna *et al*., 2019). COI is considered the most informative marker for species-level identification in both free-living and parasitic copepods (Tang *et al*., 2012; Mayor *et al*., 2017) and is often the only marker capable of resolving closely related taxa. However, amplification success varies among ergasilid and lernaeid genera, and several species show substantial intraspecific divergence that may obscure species boundaries (Míč *et al*., 2024, 2025). Current evidence indicates that combined analyses of COI and 28S provide the most reliable basis for phylogenetic inference and species delimitation across parasitic copepods (Wu *et al*., 2025).

Despite these advances, molecular coverage remains limited. GenBank currently contains 497 sequences attributable to Ergasilidae, representing 41 identified species, with additional accessions determined only at genus or family level. Sequences are heavily concentrated in a small subset of taxa, notably *Neoergasilus japonicus* (61 accessions), *Sinergasilus major* (48), *S. undulatus* (43), *Acusicola margulisae* (40), *S. polycolpus* (39) and *Ergasilus briani* (18). Additional ergasilid sequences, mainly derived from environmental sampling in the Nearctic, are available in BOLD. Taken together, any kind of molecular data exist for 13 genera and 47 valid species of Ergasilidae. For Lernaeidae, GenBank lists 346 sequences, nearly half of which correspond to *Lernaea cyprinacea* (201 accessions), followed by *Lernaea polymorpha* (44), *Lamproglena monodi* (43), *Lernaea ctenopharyngodontis* (34), *Lamproglena clariae* (21), *Lamproglena pulchella* (21), *Lernaea cruciata* (18) and *Lamproglena orientalis* (13). Additional records are available for *Lamproglena chinensis*, *Lamproglena cleopatra*, *Lamproglena hoi*, *Lamproglena hemprichii* and *Pseudolamproglena zahrziensis*, whereas a small number of sequences are assigned only to family or genus level. BOLD contains mainly sequences of *L. cyprinacea* and undetermined *Lernaea*. Overall, molecular data are available for 3 genera and 13 valid species of Lernaeidae.

In proportional terms, only 14% of ergasilid species and 10% of lernaeid species possess any molecular sequence data. Several genera remain entirely unsequenced, and representation

is strongly biased towards East Asian, European and some Neotropical lineages, whereas large portions of Africa, South Asia, Australasia, the Nearctic and many Neotropical genera of both families remain poorly sampled. These gaps restrict the development of robust phylogenetic hypotheses and highlight the need for coordinated sequencing integrated with modern redescriptions of poorly known taxa. Among the 29 valid ergasilid genera, any kind of molecular data are currently available for 13 genera (*Acusicola*, *Dermoergasilus*, *Ergasilus*, *Gamispatulus*, *Gamispinus*, *Miracetyma*, *Neoergasilus*, *Paeonodes*, *Paraergasilus*, *Rhinergasilus*, *Sinergasilus*, *Therodamas* and *Thersitina*). Among the 19 lernaeid genera, molecular data are available for three (*Lamproglena*, *Lernaea* and *Pseudolamproglena*). Overall, only 14% of all Ergasilidae and 10% of all Lernaeidae species have any sequence data available.

Table 1 List of available molecular data for families Ergasilidae and Lernaeidae, including their host family, collection locality, and accession numbers for partial 18S, 28S rDNA and COI sequences from database GenBank and Bold (indicated with *).

Parasite species	Host family	Locality	GenBank/Bold accession numbers			Reference
			18S	28S	COI	
Ergasilidae						
Acusicola margulisae	Cichlidae	Nicaragua	MN852694 - MN852696	MN852849 - MN852851	MN85438 - MN85470	Santacruz *et al.* (2020)
Dermoergasilus madagascarensis	Cichlidae	Madagascar	PP115568	PP115569	PP117929 - PP117934	Míč *et al*. (2024)
Ergasilus anchoratus	Bagridae	China	DQ107564	DQ107528	-	Song *et al.* (2008)
Ergasilus arenalbus	Tetraodontidae	South Africa	PQ451954, PQ451956	PQ451957 - PQ451958	PQ439339	van der Spuy *et al*. (2025)
Ergasilus auritus	Gasterosteidae	Canada	-	-	ECTCR091*	-
Ergasilus barbi	Cyprinidae	Turkey	PX000625	PX000652	-	Míč *et al*. (2025)
Ergasilus briani	Cobitidae	China	DQ107572	DQ107532	-	Song *et al.* (2008)
	Leuciscidae, Gobionidae	Turkey, Bosnia and Herzegovina, Croatia, Greece	PX000626 - PX000630	PX000653 - PX000657	PV988324 - PV988328	Míč *et al*. (2025)
Ergasilus caeruleus	Centrarchidae, Cichlidae	Canada; USA	-	-	ECTCR003*, ECTCR005* -ECTCR008*, ZOOPS258* -ZOOPS260*, ZOOPS351*, ZOOPS353*, ZOOPS432*, ZOOPS433*	-
Ergasilus caparti	Cichlidae	Burundi	OQ407468	OQ407472	-	Míč *et al*. (2023)
Ergasilus centrarchidarum	Centrarchidae	Canada; USA	-	-	ECTCR001*, ECTCR009*, ECTCR037*, ECTCR038* ECTCR052* - ECTCR055*, ZOOPS071* - ZOOPS075*	-
Ergasilus chautauquaensis	-	USA	-	-	ZOOPS076* - ZOOPS078*	-
Ergasilus chintensis	Tetraodontidae	South Africa	PQ451955	PQ451959	PQ439340	van der Spuy *et al*. (2025)
Ergasilus hypomesi	Gobiidae	China	DQ107573	DQ107539	-	Song *et al.* (2008)
Ergasilus italicus	Leuciscidae	Italy	PX000631	PX000658	-	Míč *et al*. (2025)
Ergasilus jaraquensis	-	-	-	-	MF651988, MF651989	Lima *et al*. (2017) unpublished
Ergasilus kandti	Cichlidae	Zambia	PQ249839	PQ249840 - PQ249843	-	Jansen *et al*. (2025)

Ergasilus labracis	-	Canada	-	-	PQ663820	Murray & Hobbs (2024) unpublished
Ergasilus lizae	Fundulidae	Canada	-	-	ECTCR024* - ECTCR026*, ECTCR039*	-
	Muglidae	Mexico	-	-	PP239046 - PP239048	Morales-Serna *et al*. (2024)
	Cyprinidae	Greece	PX000632 - PX000633	PX000659 - PX000660	PV988329 - PV988331	Míč *et al*. (2025)
Ergasilus luciopercarum	Percidae	Canada; USA	-	-	ECTCR078* - ECTCR080*, ZOOPS060* - ZOOPS064*, ZOOPS628* - ZOOPS630*	-
Ergasilus macrodactylus	Cichlidae	Burundi	OQ407465	OQ407470	-	Míč *et al*. (2023)
Ergasilus megacheir	Cichlidae	Burundi	OQ407466	OQ407471	-	Míč *et al*. (2023)
Ergasilus megaceros	-	USA	-	-	ZOOPS065* - ZOOPS070*, ZOOPS257*, ZOOPS437* - ZOOPS441*	-
Ergasilus mirabilis	Clariidae	South Africa, Zambia	OR449753, OR449754	OR449755, OR449756	OR448769, OR448770	Fikiye *et al*. (2023)
Ergasilus parasarsi	Cichlidae	Burundi	OQ407467	OQ407473	-	Míč *et al*. (2023)
Ergasilus parasiluri	Bagridae	China	DQ107567, DQ107568	DQ107536, DQ107537	-	Song *et al.* (2008)
Ergasilus parvitergum	-	India	-	-	OP871074	Reshmi & Kappali (2022) unpublished
Ergasilus parvus	Cichlidae	Burundi	OQ407469	OQ407474	-	Míč *et al*. (2023)
Ergasilus peregrinus	Sinipercidae	China	DQ107577	DQ107531	-	Song *et al.* (2008)
Ergasilus rostralis	Cyprinidae	Iraq	PX000634	PX000661	PV988332- PV988334	Míč *et al*. (2025)
Ergasilus scalaris	Bagridae	China	DQ107565, DQ107566	DQ107538	-	Song *et al.* (2008)
Ergasilus sieboldi	Percidae	Czech Republic	MW810238	MW810242	-	Kvach *et al.* (2021)
	Spaidae	Egypt	-	OM812074, ON706996	-	Abdel-Radi *et al*. (2022)
	Centrarchidae	Italy	-	PQ804730	-	Sgroi (2024) unpublished
	Ictaluridae	Czech Republic	-	PQ100627 - PQ100630	-	Ondračková *et al*. (2025b)
Ergasilus tumidus	Acheilognathidae	China	DQ107569, DQ107570, DQ107571	DQ107533, DQ107534, DQ107535	-	Song *et al.* (2008)
Ergasilus versicolor	-	USA	-	-	ZOOPS261* - ZOOPS265*	-
Ergasilus wilsoni	-	South Korea	KR048765	KR048843	KR049036	Baek *et al*. (2016)
Ergasilus yaluzangbus	Cyprinidae	Tibet	DQ107578	DQ107540	-	Song *et al.* (2008)

Ergasilus sp.	Cyprinodontidae	Mexico	-	PP919657 - PP919658	-	Espínola-Novelo *et al*. (2023)
Gamispatulus schizodontis	Serrasalmidae	Brazil	PQ452576 - PQ452577	PQ452579	PQ442938, PQ442940 - PQ442941, PQ442981	Narciso *et al*. (2024)
Gamispinus diabolicus	-	-	MF651976, MF651977, MF651978	-	MF651982, MF651983	Lima *et al*. (2017) unpublished
Miracetyma sp.	-	-	MF651979 - MF651981	-	MF651984 - MF651987	Lima *et al*. (2017) unpublished
Neoergasilus africanus	Clariidae	South Africa	PP864457 - PP864459	PP864460 - PP864461	PP866728 - PP866729	Fikiye *et al*. (2024)
Neoergasilus japonicus	-	South Korea	KR048752	KR048823	KR049037	Baek *et al*. (2016)
	Centrarchidae	Czech Republic	MH167969, MH167970	MH167967, MH167968	-	Ondračková *et al.* (2019)
	Centrarchidae, Leuciscidae	Czech Republic	MW810236, MW810237	MW810240, MW810241	-	Kvach *et al.* (2021)
	-	USA	-	-	MZ964932 - MZ964936	Vasquez *et al.* (2022)
	-	USA	-	-	OP830068	Marshall *et al*. (2019)
	Centrarchidae, Cichlidae, Cyprinidae	South Africa	OR350594 - OR350600	OR347574 - OR347582	-	Avenant-Oldewage *et al*. (2023)
	Ictaluridae	Czech Republic		PQ100638, PQ100639		Ondračková *et al.* (2025b)
	Leuciscidae	Iraq, Italy, Croatia	PX000635 - PX000638	PX000662 - PX000665	PV988335 - PV988337	Míč *et al*. (2025)
	Centrarchidae, Leuciscidae, Pericdae	Portugal	PX468607 - PX468608	PX467162 - PX467169	PX468635 - PX468639	Tkachenko *et al*. (2025)
Paeonodes subviridis	-	India	-	-	OP425700	Reshmi & Kappali (2022) unpublished
Paraergasilus brevidigitus	Cyprinidae	China	DQ107576	DQ107530	-	Song *et al.* (2008)
Paraergasilus longidigitus	Leuciscinae, Percidae,	Czech Republic	MW810239	MW810243	-	Kvach *et al.* (2021)
Paraergasilus medius	Xenocyprididae	China	DQ107574, DQ107575	DQ107529	-	Song *et al.* (2008)
Rhinergasilus piranhus	Characidae	Brazil	-	PQ452578 - PQ452581	PQ442939	Narciso *et al*. (2025)
Sinergasilus major	Xenocyprididae,	China	DQ107558 - DQ107560	DQ107524	-	Song *et al.* (2008)

	Siluridae	Hungary	MZ047814	MZ047815	-	Dos Santos *et al.* (2021)
Sinergasilus polycolpus	Xenocyprididae	China	DQ107563	DQ107525	-	Song *et al.* (2008)
	Xenocyprididae	China	-	-	KR263117 (mitochondrion)	Feng *et al.* (2016)
Sinergasilus undulatus	Cyprinidae	China	DQ107561, DQ107562	DQ107526, DQ107527	-	Song *et al.* (2008)
	-	China	-	-	MW080644 (mitochondrion)	Hua *et al.* (2021)
Therodamas longicollum	Anostomidae	Brazil	MW652731	-	-	Oliveira *et al.* (2021)
Thersitina gasterostei	-	Canada	-	-	ECTCR063*, ECTCR109*	-
Lernaeidae						
Lamproglena chinensis	Channidae	China	DQ107553, DQ328767	DQ107545	-	Song *et al.* (2008)
	-	China	MZ575117, OP076957	-	-	Hua (2021) unpublished
Lamproglena clariae	Clariidae	Kenya	OR242503 - OR242504	OR338195 - OR338196,	OR232208 - OR232209	Rindoria *et al*. (2023)
	Clariidae	South Africa	OR048797 - OR048801	OR048803 - OR048807	OR058772 - OR058776	Dos Santos *et al*. (2023)
Lamproglena cleopatra	Cyprinidae	Kenya	OR242501 - OR242502	OR338169 - OR338170	OR232207	Rindoria *et al*. (2023)
Lamproglena hemprichii	Alestidae	Zimbabwe	OP277526	OP277527	OR058777	Mabika *et al*. (2022)
Lamproglena hoi	Cyprinidae	South Africa	OR048802	OR048808	OR058778	Dos Santos *et al*. (2023)
Lamproglena monodi	Cichlidae, Percidae	Egypt, Kenya	ON419422 - ON419426, ON419438 - ON419452	ON419427 - ON419437	-	Rindoria *et al*. (2022)
	Cichlidae	Kenya	-	-	OR058779 - OR058788	Dos Santos *et al*. (2023)
Lamproglena orientalis	Xenocyprididae	China	DQ107549 - DQ107552	DQ107541 - DQ107544	-	Song *et al.* (2008)
Lamproglena pulchella	Cyprinidae, Gobionidae, Leuciscidae	Turkey, Italy, Bosnia and Herzegovina, Greece	PX000639 - PX000645	PX000666 - PX000674	PV988338 - PV988340	Míč *et al*. (2025)
Lernaea cruciata	Poeciliidae	China	MW772232, MH982199 - MH982203	MH982211 - MH982215	MH982223 - MH982227	Hua *et al*. (2019)
	-	Pakistan	PQ593646	-	-	Shafiq (2024) unpublished
	-	India	PQ013726	-	-	Saikia *et al*. (2024) unpublished
Lernaea ctenopharyngodontis	Cyprinidae	China	MK733998 - MK734006, MK336642 - MK336647	MK742748 - MK742756	MK770185 - MK770190	Hua *et al*. (2019)
	-	Pakistan	ON693283	-	-	Ashraf *et al*. (2022)

	-	Pakistan	PQ593529	-	-	Shafiq (2024) unpublished
	-	China	PP411925	-	-	Zhang (2024) unpublished
Lernaea cyprinacea	Cyprinidae	China	DQ107554 - DQ107557	DQ107546 - DQ107548	-	Song *et al.* (2008)
	Plecoglossidae	Japan	KP235363	KP235364	-	Yoshimine *et al.* (2014) unpublished
	Centrarchidae	Romania	-	KF751648 - KF751649	-	Stavrescu-Bedivan *et al.* (2014)
	Cyprinidae	Iran	KM281816	KM281817	-	Tabaripour & Youssefi (2014) unpublished
	Cyprinidae	Egypt	KX258625	KX258626	-	Abu-Elala *et al*. (2018)
	Cyprinidae	Australia	-	KY346866 - KY346868	-	McCredden (2016)
	Cichlidae	South Africa	KY435939	-	-	Welicky *et al*. (2017)
	Cyprinidae	China	MH982192 - MH982198	MH982204 - MH982210	MH982216 - MH982222	Hua *et al*. (2019)
	Atherinopsidae	Argentina	-	KX908211	-	Soares *et al*. (2018)
	Cyprinidae	China	MK336635 - MK336641, MK733991 - MK733997	MK742741 - MK742747	MK770175 - MK770183	Hua *et al*. (2019)
	Anabantidae	South Africa	MN243682	-	-	Chakona *et al*. (2019)
	Percichthyidae	Argentina	MH198049 - MH198054	-	-	Waicheim *et al*. (2019)
	Cyprinidae	India	-	MK775592, MK775556, MK738112	-	Uma *et al*. (2019) unpublished
	-	Australia	MT367688 - MT367705	MT371347 - MT371367	MT371895 - MT371909	Zhu *et al*. (2020)
	-	Russia	-	MW423693 - MW423694	-	Vlasenko & Kashinskaya (2020) unpublished
	Cyprinidae	Egypt	-	-	OL660670	Attia *et al*. (2022)
	-	India	OP050160	-	-	Praveenraj *et al.* (2022) unpublished
	-	Pakistan	ON693284	-	-	Ashraf *et al.* (2022) unpublished
	-	India	OM909073	-	-	Sarkar *et al*. (2022)
	Cyprinidae	India	-	OM835790, OM827069 - OM827070	-	Nirosha *et al*. (2022)
	-	Austria	-	-	PAVEA148* - PAVEA151*	-

	Poecillidae	Iran	OP175983	-	-	Rahmati-Holasoo *et al*. (2023)
	Cyprinidae	Indonesia	OP895710	OP902215 - OP902216	-	Prastowo *et al*. (2023)
		Uzbekistan	OR643687, OR643672	-	-	Nomonov *et al*. (2023)
	Cyprinidae	India	OR373058	OR381184	-	Tripathi *et al*. (2023) unpublished
	-	Iraq	OQ195267 - OQ195270	-	OR431748	Mohammed & Abdullah (2023) unpublished
	Poecillidae	India	-	-	OR800156	Das *et al*. (2023) unpublished
	-	USA	-	-	OQ872369	Gerth (2023) unpublished
	Ranidae (Amphibia)	China	PP077251	-	-	He (2024) unpublished
	Cyprinidae	Egypt	-	-	PP421062	Ramadan (2024) unpublished
	-	India	PQ008642	-	-	Saikia *et al*. (2024)
	-	Pakistan	PQ594185, PQ216010	-	-	Shafiq (2024) unpublished
	Esocidae	Russia	OR945736 - OR945737	OR947420	OR945731 - OR945732	Kuznetsova *et al*. (2024) unpublished
		Iraq	-	-	PV230509 - PV230511	Karem & Abdullah (2025)
	Cyprinidae	Iraq	LC830719 - LC830722	-	-	Jameel *et al*. (2025)
	Cyprinidae, Leuciscidae	Turkey, Bosnia and Herzegovina, Spain	PX000646 - PX000650	PX000675 - PX000679	PV988342 - PV988345	Míč *et al*. (2025)
Lernaea polymorpha	Cyprinidae	China	MK734007 - MK734016, MK336648 - MK336657, ON693285	MK742757 - MK742766	MK770191 - MK770200	Hua *et al*. (2019)
	-	Pakistan	PQ591794, PQ593502	-	-	Shafiq (2024) unpublished
Pseudolamproglena zahrziensis	Cyprnidiae	Iraq	PX000651	PX000680	PV988346 - PV988349	Míč *et al*. (2025)

Discussion and future prospects

The global patterns of diversity and distribution documented here must be interpreted with caution, as they are strongly shaped by uneven historical sampling rather than by biological aspects alone. Records of Ergasilidae and Lernaeidae are concentrated in regions and host groups that attracted sustained attention from a limited number of taxonomists, while geographic areas and fish assemblages remain poorly explored. Apparent centres of diversity in the Neotropics, the Oriental region and parts of Africa therefore reflect both genuine evolutionary radiations and a long history of focused taxonomic activity, whereas regions such as the Pacific Oceanic Islands, large parts of Australasia, central Africa and portions of South America remain effectively unsampled.

At a global scale, the contrasting distributions of Ergasilidae and Lernaeidae reflect a combination of historical biogeography, host availability, and uneven taxonomic effort rather than simple ecological determinants. The exceptional richness of Ergasilidae in the Neotropical region is consistent with earlier syntheses of freshwater copepod diversity, which identified Amazonia as a major centre of endemic radiation for multiple copepod lineages (Boxshall & Defaye, 2008). Within Ergasilidae, most Neotropical genera form a monophyletic lineage that diversified extensively within the Amazon Basin, likely facilitated by the long term stability and hydrological connectivity of lowland river systems, which promote both host diversification and parasite isolation. In contrast, Lernaeidae exhibit their highest diversity in the Oriental and Afrotropical regions, a pattern previously attributed to an early radiation associated with cyprinid hosts on the Indian subcontinent, followed by dispersal into Africa and Eurasia during the northward movement of the Indian plate (Ho, 1998). This scenario is supported by the concentration of endemic lernaeid genera in Asia and Africa and by the absence or low diversity of the family in regions lacking extensive native cyprinid faunas, such as Australasia and the Pacific Oceanic Islands. At the same time, these broad scale patterns are amplified by strong sampling biases. Regions with long traditions of freshwater parasitology, including Europe, East Asia, and parts of South America, are disproportionately represented, whereas large areas of Africa, Australasia and the Pacific islands remain poorly surveyed. As emphasized for freshwater copepods in general, apparent centres of diversity therefore reflect both genuine evolutionary radiations and the historical focus of taxonomic research, and should be interpreted with caution in the absence of more even global sampling

Taxonomic practice has further contributed to the heterogeneity of the available data. In some regions and historical periods, newly collected material was routinely assigned to

previously described species with limited critical comparison, leading to probable underestimation of diversity. In contrast, other traditions favoured the description of new species based on minor morphological differences, often without adequate consideration of intraspecific variability. This contrast is particularly evident in Lernaeidae and is most pronounced in the genus *Lernaea*, where extreme plasticity of the female holdfast has resulted in the proliferation of nominal species and subspecies based on local morphotypes (Harding, 1950). Accumulating molecular evidence indicates that several of these nominal taxa fall within the variation of *L. cyprinacea*, suggesting that many subspecies and closely similar species are unlikely to represent independent evolutionary lineages (Hua *et al*., 2019). At the same time, the taxonomic situation is severely constrained by the absence of type material and the inadequacy of the original description of *L. cyprinacea*, making comparative assessment of historical names extremely difficult. A comprehensive revision of *L. cyprinacea* sensu lato, incorporating redescribed reference material and molecular data, is therefore essential before any stable species boundaries can be proposed.

Conversely, several species currently treated as widely distributed almost certainly represent complexes of morphologically similar taxa. In Ergasilidae, this problem was already recognised by El-Rashidy (1999), who suggested that *E. lizae* does not represent a single homogeneous species but a set of closely related forms occurring in different parts of its reported range. Subsequent records from widely separated regions have continued to rely on this name (Morales-Serna *et al*., 2024). A comparable situation is now apparent in Lernaeidae. Recent molecular data for *Lamproglena pulchella* show genetic divergence among populations assigned to this species across different regions (Míč *et al*., 2025), despite their overall morphological similarity. These cases indicate that several widely reported taxa in both families may conceal cryptic diversity.

Despite more than two centuries of study, both families continue to yield new species, including in regions that have long histories of parasitological research, such as the recent descriptions of *N. africanus* in South Africa or *E. italicus* in Italy (Fikiye *et al*., 2024; Míč *et al*, 2025). This shows that current diversity estimates remain provisional and that undiscovered taxa almost certainly persist across all major biogeographical realms. When new species are described, molecular data should be included alongside detailed morphological descriptions whenever possible. This integrative approach facilitates future comparisons and allows historical material to be reassessed.

At the generic level, phylogenetic relationships within Ergasilidae and Lernaeidae remain insufficiently resolved and the polyphyletic status of *Ergasilus* persists (Míč *et al.*, 2025; Narciso *et al*., 2025). Molecular sampling is strongly biased toward a small number of widespread or invasive species and a limited subset of genera, leaving most lineages entirely unsampled. Targeted sequencing aimed at maximising generic coverage, rather than repeatedly sampling already well represented taxa, are therefore required. Until a substantially broader phylogenetic framework is available, major restructuring of generic boundaries would be premature and risks introducing further instability into families that are already taxonomically complex.

Conclusion

The global review presented here provides a necessary baseline for understanding diversity, host associations and distribution of Ergasilidae and Lernaeidae. Progress in understanding these families will depend primarily on the re-examination of historically and poorly known taxa, incorporation of molecular data into species descriptions, and improved sampling in regions that remain largely unexplored. At present, phylogenetic coverage remains too limited to support robust conclusions regarding relationships within and between genera. Expanded integrative studies combining morphology and molecular data are therefore required to stabilise nomenclature and clarify the evolutionary structure of both families.

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Author contributions

RM and MS conceived and designed the study. RM compiled the dataset and wrote the first draft of the manuscript. All authors substantially contributed to the final draft and approved the final version of the manuscript.

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Competing interests

The authors declare there are no conflicts of interest.

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Supplementary material

Supplementary Table 1 Checklist of all valid species of Ergasilidae, including recognised synonyms, with their documented distribution across biogeographical regions and known host associations.

Species	PA	NA	NT	AT	OL	AU	PAC	ANT	Hosts
Abergasilus amplexus Hewitt, 1978	–	–	–	–	–	X	–	–	Anguilliformes, Cypriniformes, Gadiformes, Galaxiiformes, Osmeriformes, Perciformes, Pleuronectiformes, Scombriformes
Acusicola brasiliensis Amado & Rocha C.E.F., 1996	–	–	X	–	–	–	–	–	Atheriniformes, Clupeiformes, Mugiliformes
Acusicola cunula Cressey, in Cressey & Collette, 1970	–	–	X	–	–	–	–	–	Beloniformes
Acusicola iamarinoi Couto, Pereira, Luque, Paschoal & Pereira, 2022	–	–	X	–	–	–	–	–	Acanthuriformes
Acusicola joturicola El-Rashidy & Boxshall, 1999	–	–	X	–	–	–	–	–	Mugiliformes
Acusicola lycengraulidis Thatcher & Boeger, 1983	–	–	X	–	–	–	–	–	Clupeiformes
Acusicola margulisae Santacruz, Morales-Serna, Leal-Cardín, Barluenga & de León, 2020	–	–	X	–	–	–	–	–	Cichliformes, Cyprinodontiformes
Acusicola mazatlanesis El-Rashidy & Boxshall, 1999	–	–	X	–	–	–	–	–	Mugiliformes
Acusicola minuta Araujo & Boxshall, 2001	–	–	X	–	–	–	–	–	plankton
Acusicola paracunula Amado & Rocha C.E.F., 1996	–	–	X	–	–	–	–	–	Beloniformes, Clupeiformes
Acusicola pasternakae Couto, Pereira, Luque, Paschoal & Pereira, 2022	–	–	X	–	–	–	–	–	Carangaria/misc
Acusicola pellonidis Thatcher & Boeger, 1983	–	–	X	–	–	–	–	–	Clupeiformes, Characiformes
Acusicola rochai Couto, Nunes, Paschoal & Pereira, 2024	–	–	X	–	–	–	–	–	Cyprinodontiformes
Acusicola rogeri Amado & Rocha C.E.F., 1996	–	–	X	–	–	–	–	–	Beloniformes
Acusicola rotunda Amado & Rocha C.E.F., 1996	–	–	X	–	–	–	–	–	Clupeiformes
Acusicola spinuloderma El-Rashidy & Boxshall, 1999	–	–	X	–	–	–	–	–	Mugiliformes
Acusicola spinulosa Amado & Rocha C.E.F., 1996	–	–	X	–	–	–	–	–	Clupeiformes
Acusicola tenax (Roberts, 1965) (= *Ergasilus tenax* Roberts, 1965)	–	X	–	–	–	–	–	–	Centrarchiformes, Esociformes
Acusicola tucunarense Thatcher, 1984	–	–	X	–	–	–	–	–	Cichliformes
Amplexibranchius bryconis Thatcher & Paredes, 1985	–	–	X	–	–	–	–	–	Characiformes
Brasergasilus anodus Thatcher & Boeger, 1983	–	–	X	–	–	–	–	–	Characiformes
Brasergasilus bifurcatus Santos, Thatcher & Brasil-Sato, 2007	–	–	X	–	–	–	–	–	Characiformes
Brasergasilus guaporensis Malta, 1995	–	–	X	–	–	–	–	–	Characiformes
Brasergasilus jaraquensis Thatcher & Boeger, 1983	–	–	X	–	–	–	–	–	Characiformes
Brasergasilus mamorensis Varella & Malta, 2001	–	–	X	–	–	–	–	–	Characiformes
Brasergasilus oranus Thatcher & Boeger, 1985	–	–	X	–	–	–	–	–	Characiformes

Species	PA	NA	NT	AT	OL	AU	PAC	ANT	Hosts
Dermoergasilus amplectens (Dogiel & Akhmerov, 1952) (= *Ergasilus amplectens* Dogiel & Akhmerov, 1952)	X	–	–	X	X	X	–	–	Acanthuriformes, Beloniformes Cichliformes, Elopiformes, *Eupercaria* (Gerreidae), Gonorynchiformes, Mugiliformes,
Dermoergasilus cichlidus Ali & Adday, 2019	–	–	–	–	–	X	–	–	Cichliformes
Dermoergasilus coleus (Cressey in Cressey & Collette, 1970) (= *Ergasilus coleus* Cressey in Cressey & Collette, 1970)	–	–	–	–	X	–	–	–	Beloniformes
Dermoergasilus curtus El-Rashidy & Boxshall, 2001	–	–	–	–	X	–	–	–	Mugiliformes
Dermoergasilus intermedius (Kabata, 1992) (= *Ergasilus intermedius* Kabata, 1992)	–	–	–	–	–	X	–	–	Centrarchiformes, Clupeiformes, Siluriformes
Dermoergasilus kabatai (Thomas, 1994) (= *Ergasilus kabatai* Thomas, 1994)	–	–	–	–	X	–	–	–	Mugiliformes
Dermoergasilus longiabdominalis El-Rashidy & Boxshall, 2001	–	–	–	X	X	–	–	–	Mugiliformes
Dermoergasilus madagascarensis Míč, Řehulková, Šimková & Seifertová. 2024	–	–	–	X	–	–	–	–	Cichliformes
Dermoergasilus mugilis Oldewage & van As, 1988	–	–	–	X	–	–	–	–	Mugiliformes
Dermoergasilus occidentalis Hassan, Jones & Lymbery, 2009	–	–	–	–	–	X	–	–	Galaxiiformes, Siluriformes
Dermoergasilus planilizai n. sp.	X	–	–	–	–	–	–	–	Mugiliformes
Dermoergasilus semiamplectens El-Rashidy & Boxshall, 2001	X	–	–	–	X	–	–	–	Mugiliformes
Dermoergasilus semicoleus (Cressey in Cressey & Collette, 1970) (= *Ergasilus semicoleus* Cressey in Cressey & Collette, 1970)	–	–	–	–	–	X	–	–	Beloniformes
Dermoergasilus varicoleus Ho, Jayarajan & Radhakrishan, 1992	X	–	–	–	X	–	–	–	Mugiliformes, Cypriniformes, Siluriformes
Duoergasilus basilongus Narciso, Brandão, Perbiche-Neves & da Silva, 2019	–	–	X	–	–	–	–	–	Characiformes
Ergasilus acusicestraeus El-Rashidy & Boxshall, 1999	–	–	–	–	–	X	–	–	Mugiliformes
Ergasilus amblycephalus Kuang, in Kuang & Qian, 1983	–	–	–	–	X	–	–	–	Cypriniformes
Ergasilus anchoratus Markevich, 1946	X	–	–	–	X	–	–	–	Cypriniformes; Siluriformes; Tetraodontiformes
Ergasilus arenalbus van der Spuy, Narciso, Hadfield, Wepener & Smit, 2024	–	–	–	X	–	–	–	–	Tetraodontiformes
Ergasilus argulus Cressey in Cressey & Collette, 1970	–	–	X	–	–	–	–	–	Beloniformes
Ergasilus arthrosis Roberts, 1969	–	X	–	–	–	–	–	–	Atheriniformes; Carangiformes; Centrarchiformes; Clupeiformes; Eupercaria/misc; Perciformes/Percoidei; Percopsiformes; Pleuronectiformes; Siluriformes
Ergasilus atafonensis Amado & Rocha, 1996	–	–	X	–	–	–	–	–	Mugiliformes
Ergasilus auritus Markevich, 1940	X	X	–	–	–	–	–	–	Gobiiformes; Osmeriformes; Perciformes/Cottoidei; Perciformes/Gasterosteoidei; Salmoniformes

Species	PA	NA	NT	AT	OL	AU	PAC	ANT	Hosts
Ergasilus australiensis Roubal, 1981	–	–	–	–	–	X	–	–	Carangaria/misc; Eupercaria/misc; Mugiliformes
Ergasilus bagarii Kuang, in Kuang & Qian, 1983	–	–	–	–	X	–	–	–	Siluriformes
Ergasilus bahiensis Amado & Rocha, 1996	–	–	X	–	–	–	–	–	Mugiliformes; Siluriformes
Ergasilus bani Ohtsuka, Ho & Nagasawa, 2004	X	–	–	–	–	–	–	–	plankton
Ergasilus barbi Rahemo, 1982	X	–	–	–	–	–	–	–	Cypriniformes; Mugiliformes; Siluriformes
Ergasilus batai Karamchandani, 1952	–	–	–	–	X	–	–	–	Cypriniformes
Ergasilus bengalensis Southwell & Prashad, 1918	–	–	–	–	X	–	–	–	Siluriformes
Ergasilus boettgeri Reichenbach-Klinke, 1958	X	–	–	–	–	–	–	–	Cyprinodontiformes
Ergasilus boleophthalmi Adday & Ali, 2011	X	–	–	–	–	–	–	–	Gobiiformes
Ergasilus borneoensis Yamaguti, 1954	–	–	–	–	X	–	–	–	Perciformes/Serranoidei
Ergasilus brari Battish & Brar, 1990	–	–	–	–	X	–	–	–	Siluriformes
Ergasilus briani Markevich, 1933 (= *Ergasilus minor* Halisch, 1934)	X	–	–	–	–	–	–	–	Cypriniformes; Eupercaria/misc; Gobiiformes; Osmeriformes; Perciformes/Percoidei; Salmoniformes; Siluriformes
Ergasilus bryconis Thatcher, 1981	–	–	X	–	–	–	–	–	Characiformes
Ergasilus caeruleus Wilson C.B., 1911	–	X	–	–	–	–	–	–	Centrarchiformes; Cypriniformes; Cyprinodontiformes; Eupercaria/misc; Lepisosteiformes; Perciformes/Percoidei; Percopsiformes; Petromyzontiformes; Salmoniformes
Ergasilus callophysus Thatcher & Boeger, 1984	–	–	X	–	–	–	–	–	Siluriformes
Ergasilus caparti Míč, Řehulková & Seifertová, 2023	–	–	–	X	–	–	–	–	Cichliformes
Ergasilus caraguatatubensis Amado & Rocha, 1996	–	–	X	–	–	–	–	–	Mugiliformes
Ergasilus celestis Mueller J.F., 1937 (= *Ergasilus osburni* Tidd & Bangham, 1945)	–	X	–	–	–	–	–	–	Anguilliformes; Gadiformes
Ergasilus centrarchidarum Wright R., 1882 (= *Ergasilus nigritus* Wilson C.B., 1916)	–	X	–	–	–	–	–	–	Centrarchiformes; Cypriniformes; Eupercaria/misc; Gadiformes; Osmeriformes; Perciformes/Percoidei
Ergasilus cerastes Roberts, 1969	–	X	–	–	–	–	–	–	Siluriformes
Ergasilus ceylonensis Fernando & Hanek, 1973	–	–	–	–	X	–	–	–	Cichliformes; Cypriniformes; Cyprinodontiformes
Ergasilus chautauquaensis Fellows, 1887	–	X	–	–	–	–	–	–	plankton
Ergasilus chelangulatus Thatcher & Brasil-Sato, 2008	–	–	X	–	–	–	–	–	Siluriformes
Ergasilus chintensis van der Spuy, Narciso, Hadfield, Wepener & Smit, 2024	–	–	–	X	–	–	–	–	Tetraodontiformes
Ergasilus clupeidarum Johnson S.K. & Rogers, 1972	–	X	–	–	–	–	–	–	Clupeiformes; Siluriformes
Ergasilus coatiarus Araujo & Varella, 1998	–	–	X	–	–	–	–	–	Characiformes; Cichliformes
Ergasilus cochlearius Kuang & Liu, 1991	–	–	–	–	X	–	–	–	Siluriformes

Species	PA	NA	NT	AT	OL	AU	PAC	ANT	Hosts
Ergasilus colomesus Thatcher & Boeger, 1983	–	–	X	–	–	–	–	–	Tetraodontiformes
Ergasilus coniformis Kim I.H. & Choi, 2003	X	–	–	–	–	–	–	–	Cypriniformes
Ergasilus cotti Kellicott, 1892	–	X	–	–	–	–	–	–	Perciformes/Cottoidei; Perciformes/Percoidei
Ergasilus cunningtoni Capart, 1944	–	–	–	X	–	–	–	–	Characiformes; Cichliformes; Clupeiformes; Cypriniformes; Osteoglossiformes; Siluriformes
Ergasilus curticrus Muriel-Hoyos, Santana-Pineros, Cruz-Quintana & Suarez-Morales, 2015	–	–	X	–	–	–	–	–	Characiformes
Ergasilus cyanopictus Carvalho, 1962	–	–	X	–	–	–	–	–	Mugiliformes
Ergasilus cyprinaceus Rogers, 1969	–	X	–	–	–	–	–	–	Centrarchiformes; Cypriniformes; Cyprinodontiformes; Perciformes/Gasterosteoidei; Siluriformes
Ergasilus danjiangensis Song, Yao & Nie, 2008	–	–	–	–	X	–	–	–	Cypriniformes
Ergasilus davidi Suárez-Morales & Santana-Pineros, 2008	–	X	–	–	–	–	–	–	Carangaria/misc; Eupercaria/misc
Ergasilus divergens (Kokubo, 1914) (= *Limnoncaea divergens* Kokubo, 1914)	X	–	–	–	–	–	–	–	plankton
Ergasilus ecuadorensis El-Rashidy & Boxshall, 2002	–	–	X	–	–	–	–	–	Mugiliformes
Ergasilus egyptiacus Abdel-Hady, Bayoumy & Osman, 2008	X	–	–	–	–	–	–	–	Cichliformes
Ergasilus elongatus Wilson C.B., 1916	–	X	–	–	–	–	–	–	Acipenseriformes
Ergasilus enshiensis Liu & Wang, 1997	X	–	–	–	–	–	–	–	Cypriniformes
Ergasilus extensus El-Rashidy & Boxshall, 2002	X	–	–	–	–	X	–	–	Mugiliformes
Ergasilus felichthys (Pearse, 1947) (= *Macrobrachinus felichthys* Pearse, 1947; *Ergasilus elongatus* Thomsen, 1949; *Ergasilus thomseni* Yamaguti, 1963)	–	X	X	–	–	–	–	–	Siluriformes
Ergasilus fidiformis Yamaguti, 1953	X	–	–	–	–	–	–	–	Cypriniformes
Ergasilus flaccidus Fryer, 1965	–	–	–	X	–	–	–	–	Cichliformes
Ergasilus foresti Boxshall, Araujo & Montu, 2002	–	–	X	–	–	–	–	–	plankton
Ergasilus fryeri Paperna, 1964	X	–	–	–	–	–	–	–	Anguilliformes; Cichliformes; Cypriniformes; Mugiliformes
Ergasilus funduli Krøyer, 1863	–	X	–	–	–	–	–	–	Atheriniformes; Cyprinodontiformes; Gobiiformes; Mugiliformes; Osmeriformes; Perciformes/Gasterosteoidei
Ergasilus genuinus (Kokubo, 1914) (= *Limnoncaea genuina* Kokubo, 1914)	X	–	–	–	–	–	–	–	plankton
Ergasilus gibbus von Nordmann, 1832	X	–	–	–	X	–	–	–	Anabantiformes; Anguilliformes; Cypriniformes; Gobiiformes
Ergasilus glyptothoracis Kuang, in Kuang & Qian, 1983	–	–	–	–	X	–	–	–	Siluriformes
Ergasilus gobiorum Markevich & Sukhnenko, 1967	X	–	–	–	–	–	–	–	Gobiiformes
Ergasilus hamiltoni Southwell & Prashad, 1918	–	–	–	–	X	–	–	–	Anabantiformes

Species	PA	NA	NT	AT	OL	AU	PAC	ANT	Hosts
Ergasilus hemibagri Zhang & Ma, 1994	–	–	–	–	X	–	–	–	Siluriformes
Ergasilus holobryconis Malta & Varella, 1986	–	–	X	–	–	–	–	–	Characiformes
Ergasilus hydrolycus Thatcher, Boeger & Robertson B.A., 1984	–	–	X	–	–	–	–	–	Characiformes
Ergasilus hypoatherinae Izawa, 2025	X	–	–	–	–	–	–	–	Atheriniformes
Ergasilus hypomesi Yamaguti, 1936	X	–	–	–	X	–	–	–	Beloniformes; Centrarchiformes; Clupeiformes; Cypriniformes; Gobiiformes; Osmeriformes; Tetraodontiformes
Ergasilus hypophthalmi Boeger, Martins & Thatcher, 1993	–	–	X	–	–	–	–	–	Siluriformes
Ergasilus ilani Oldewage & van As, 1988	–	–	–	X	–	–	–	–	Mugiliformes
Ergasilus inflatipes Cressey in Cressey & Collette, 1970	–	–	–	X	–	–	–	–	Beloniformes
Ergasilus iraquensis Amado in Amado, da Rocha, Piasecki, Al-Daraji & Mhaisen, 2001 (= *Ergasilus irakiensis* Al-Daraji, 2002)	X	–	–	–	–	–	–	–	Mugiliformes
Ergasilus italicus Míč, Hodová, Šimková, Benovics, Šanda, Vukić & Seifertová, 2025	X	–	–	–	–	–	–	–	Cypriniformes
Ergasilus jaraquensis Thatcher & Robertson B.A., 1982	–	–	X	–	–	–	–	–	Characiformes
Ergasilus jiangxiensis Liu, 1998	–	–	–	–	X	–	–	–	Cypriniformes
Ergasilus kandti Douwe, 1912	–	–	–	X	–	–	–	–	Carangaria/misc; Characiformes; Cichliformes; Siluriformes
Ergasilus kimi Boxshall, 2016	–	–	–	–	X	–	–	–	Myliobatiformes
Ergasilus labracis Krøyer, 1863	–	X	–	–	–	–	–	–	Eupercaria/misc; Gadiformes; Osmeriformes; Perciformes/Gasterosteoidei; Salmoniformes
Ergasilus lacusauratus Marques, Boeger & Brasil-Sato, 2015	–	–	X	–	–	–	–	–	Characiformes
Ergasilus lagunaris Grandori, 1925	X	–	–	–	–	–	–	–	plankton
Ergasilus lamellifer Fryer, 1961	–	–	–	X	–	–	–	–	Cichliformes; Siluriformes
Ergasilus lanceolatus Wilson C.B., 1916	–	X	–	–	–	–	–	–	Clupeiformes; Hiodontiformes
Ergasilus latus Fryer, 1960	–	–	–	X	X	–	–	–	Cichliformes; Mugiliformes; Siluriformes
Ergasilus leiocassi Xu, 1987	–	–	–	–	X	–	–	–	Siluriformes
Ergasilus leporinidis Thatcher, 1981	–	–	X	–	–	–	–	–	Characiformes
Ergasilus lizae Krøyer, 1863 (= *Ergasilus nanus* Beneden, 1870)	X	X	X	X	X	X	–	–	Acanthuriformes; Anguilliformes; Beloniformes; Carangaria/misc ; Carangiformes ; Centrarchiformes; Cichliformes; Clupeiformes; Cypriniformes; Cyprinodontiformes; Elopiformes; Esociformes; Eupercaria/misc; Eupercaria/misc ; Gobiiformes; Mugiliformes; Ovalentaria/misc; Perciformes; Pleuronectiformes; Salmoniformes; Siluriformes; Syngnathiformes
Ergasilus lobus Lin & Ho, 1998	–	–	–	–	X	–	–	–	Perciformes/Serranoidei

Species	PA	NA	NT	AT	OL	AU	PAC	ANT	Hosts
Ergasilus longicaudatus Kuang & Li, 1984	–	–	–	–	X	–	–	–	plankton
Ergasilus longimanus Krøyer, 1863	–	X	X	–	–	–	–	–	Mugiliformes
Ergasilus longipalpus Wilson C.B., 1913	–	–	X	–	–	–	–	–	Tetraodontiformes
Ergasilus luciopercarum Henderson, 1926 (= *Ergasilus confuses* Bere, 1931; *Ergasilus skrjabini* Mueller J.F., 1937)	–	X	–	–	–	–	–	–	Anguilliformes; Centrarchiformes; Cypriniformes; Eupercaria/misc; Gadiformes; Perciformes/Percoidei; Percopsiformes; Salmoniformes
Ergasilus ludhianata Battish, Brar, Bhalla & Kochar, 1997	–	–	–	–	X	–	–	–	Cypriniformes
Ergasilus luteusi Al-Sahlany, Adday & Ali, 2024	X	–	–	–	–	–	–	–	Cypriniformes; Mugiliformes
Ergasilus lyraephorus Couto, Nunes, Rincon, Paschoal & Pereira, 2023	–	–	X	–	–	–	–	–	Gymnotiformes
Ergasilus macrodactylus (Sars G.O., 1909) (= *Ergasiloides macrodactylus* Sars G.O., 1909)	–	–	–	X	–	–	–	–	Characiformes; Cichliformes
Ergasilus magnicornis Yin, 1949	X	–	–	–	X	–	–	–	Cypriniformes; Mugiliformes
Ergasilus malnadensis Venkateshappa, Seenappa & Manohar, 1988	–	–	–	–	X	–	–	–	Anabantiformes; Siluriformes; Synbranchiformes
Ergasilus manicatus Wilson C.B., 1911	–	X	–	–	–	–	–	–	Atheriniformes; Cyprinodontiformes; Perciformes/Gasterosteoidei
Ergasilus megaceros Wilson C.B., 1916 (= *Ergasilus fragilis* Mueller J.F., 1937)	–	X	–	–	–	–	–	–	Clupeiformes; Cypriniformes; Esociformes; Petromyzontiformes; Siluriformes
Ergasilus megacheir (Sars G.O., 1909) (= *Ergasiloides megacheir* Sars G.O., 1909)	–	–	–	X	–	–	–	–	Cichliformes; Siluriformes
Ergasilus mendisi Fernando & Hanek, 1973	–	–	–	–	X	–	–	–	Siluriformes
Ergasilus mirabilis Oldewage & van As, 1987	–	–	–	X	–	–	–	–	Characiformes; Cichliformes; Cypriniformes; Gobiiformes; Osteoglossiformes; Siluriformes
Ergasilus monodi Brian, 1927	–	–	–	X	–	–	–	–	Acanthuriformes; Pleuronectiformes; Siluriformes
Ergasilus mosulensis Rahemo, 1982	X	–	–	–	–	–	–	–	Cichliformes; Cypriniformes; Eupercaria/misc ; Mugiliformes; Siluriformes; Synbranchiformes
Ergasilus mugilis Vogt, 1877	X	X	–	–	–	–	–	–	Elopiformes; Eupercaria/misc; Mugiliformes
Ergasilus myctarothes Wilson C.B., 1913	–	–	X	–	–	–	–	–	Carcharhiniformes
Ergasilus nerkae Roberts, 1963	–	X	–	–	–	–	–	–	Centrarchiformes; Cypriniformes; Perciformes/Cottoidei; Perciformes/Gasterosteoidei; Percopsiformes; Salmoniformes
Ergasilus nodosus Wilson C.B., 1924	–	–	–	X	–	–	–	–	Siluriformes
Ergasilus ogawai Kabata, 1992	X	–	–	–	–	X	–	–	Carangaria/misc; Cichliformes; Clupeiformes; Cypriniformes; Eupercaria/misc; Mugiliformes; Rhinopristiformes; Siluriformes; Synbranchiformes

Species	PA	NA	NT	AT	OL	AU	PAC	ANT	Hosts
Ergasilus orientalis Yamaguti, 1939	X	–	X	–	–	X	X	–	Atheriniformes; Beloniformes; Gobiiformes; Mugiliformes
Ergasilus osmeri Beneden, 1870	X	–	–	–	–	–	–	–	Osmeriformes
Ergasilus ovatus Shen, 1957	X	–	–	–	–	–	–	–	Cypriniformes
Ergasilus pakistanicus Jafri, 1995	–	–	–	–	X	–	–	–	Synbranchiformes
Ergasilus parabahiensis El-Rashidy & Boxshall, 1999	–	–	X	–	–	–	–	–	Mugiliformes
Ergasilus pararostralis Amado in Amado, da Rocha, Piasecki, Al-Daraji & Mhaisen, 2001 (= *Ergasilus pararostralis* Al-Daraji, 2002)	X	–	–	–	–	–	–	–	Mugiliformes; Siluriformes
Ergasilus parasarsi Míč, Řehulková & Seifertová, 2023	–	–	–	X	–	–	–	–	Cichliformes
Ergasilus parasiluri (Yamaguti, 1936) (= *Pseudergasilus parasiluri* Yamaguti, 1936)	X	–	–	–	X	–	–	–	Centrarchiformes; Cypriniformes; Gobiiformes; Siluriformes
Ergasilus parvitergum Ho, Jayarajan & Radhakrishnan, 1992	–	–	–	–	X	–	–	–	Acanthuriformes; Anabantiformes; Beloniformes; Carangiformes; Centrarchiformes; Cichliformes; Clupeiformes; Eupercaria/misc; Gonorynchiformes; Mugiliformes; Ovalentaria/misc; Siluriformes; Tetraodontiformes
Ergasilus parvus Míč, Řehulková & Seifertová, 2023	–	–	–	X	–	–	–	–	Cichliformes
Ergasilus peregrinus Heller, 1865	X	–	–	–	X	–	–	–	Anabantiformes; Anguilliformes; Centrarchiformes; Cypriniformes; Gobiiformes; Mugiliformes; Salmoniformes; Siluriformes
Ergasilus philippinensis Velasquez, 1951	–	–	–	–	X	–	–	–	Centrarchiformes; Cichliformes; Gobiiformes
Ergasilus piriformis El-Rashidy & Boxshall, 2002	–	–	–	–	X	–	–	–	Mugiliformes
Ergasilus pitalicus Thatcher, 1984	–	–	X	–	–	–	–	–	Cichliformes
Ergasilus plecoglossi Yamaguti, 1939	X	–	–	–	–	–	–	–	Osmeriformes
Ergasilus polynemi Redkar, Rangnekar & Murti, 1952	–	–	–	–	X	–	–	–	Carangaria/misc
Ergasilus ponticus Markevich, 1940	X	–	–	–	–	–	–	–	Syngnathiformes
Ergasilus rhinos Burris & Miller G.C., 1972	–	X	–	–	–	–	–	–	Centrarchiformes
Ergasilus rostralis Ho, Jayarajan & Radhakrishnan, 1992	X	–	–	–	X	–	–	–	Clupeiformes; Cypriniformes; Eupercaria/misc; Mugiliformes; Siluriformes
Ergasilus rotundicorpus Jones J.B. & Hine, 1983	–	–	–	–	X	–	–	–	Acanthuriformes
Ergasilus salmini Thatcher & Brasil-Sato, 2008	–	–	X	–	–	–	–	–	Characiformes
Ergasilus sarsi Capart, 1944	X	–	–	X	X	–	–	–	Carangaria/misc; Cichliformes; Cyprinodontiformes; Mugiliformes; Osteoglossiformes; Siluriformes
Ergasilus scalaris Markevich, 1940	X	–	–	–	X	–	–	–	Centrarchiformes; Cypriniformes; Gobiiformes; Siluriformes
Ergasilus scotti Sundara Raj, 1923	–	–	–	–	X	–	–	–	Siluriformes

Species	PA	NA	NT	AT	OL	AU	PAC	ANT	Hosts
Ergasilus sergipensis Amado & Rocha C.E.F., 2001	–	–	X	–	–	–	–	–	plankton
Ergasilus shehyangensis Wang K.N., 1961	–	–	–	–	X	–	–	–	Mugiliformes
Ergasilus sieboldi von Nordmann, 1832 (= *Ergasilus trisetaceus* von Nordmann, 1832; *Ergasilus sieboldi sieboldi* von Nordmann, 1832; *Ergasilus depressus* Sars G.O., 1863; *Ergasilus esocis* Sumpf, 1871; *Ergasilus surbecki* Baumann, 1913; *Ergasilus hoferi* Borodin, 1915; *Ergasilus baicalensis* Messjatzeff, 1928)	X	–	X	–	X	–	–	–	Acanthuriformes; Acipenseriformes; Anguilliformes; Centrarchiformes; Cichliformes; Clupeiformes; Cypriniformes; Cyprinodontiformes; Esociformes; Eupercaria/misc; Gadiformes; Gobiiformes; Mugiliformes; Osmeriformes; Perciformes/Gasterosteoidei; Perciformes/Percoidei; Pleuronectiformes; Salmoniformes; Siluriformes
Ergasilus sinefalcatus Marques, Boeger & Brasil-Sato, 2015	–	–	X	–	–	–	–	–	Characiformes
Ergasilus sittangenesis El-Rashidy & Boxshall, 2002	–	–	–	–	X	–	–	–	Mugiliformes
Ergasilus spatulus Cressey in Cressey & Collette, 1970	–	X	–	–	–	–	–	–	Beloniformes
Ergasilus spinilaminatus Kabata, 1992	–	–	–	–	–	X	–	–	Centrarchiformes
Ergasilus suboculatus (Hesse, 1871) (= *Megabrachinus suboculatus* Hesse, 1871)	X	–	–	–	–	–	–	–	Mugiliformes
Ergasilus synanceiensis Amado in Amado, da Rocha, Piasecki, Al-Daraji & Mhaisen, 2001 (= *Ergasilus synanceiensis* Al-Daraji, 2002)	X	–	–	–	–	–	–	–	Perciformes/Scorpaenoidei
Ergasilus thailandensis Capart, 1943	–	–	–	–	X	–	–	–	Cypriniformes; Siluriformes
Ergasilus thatcheri Engers, Boeger & Brandao, 2000	–	–	X	–	–	–	–	–	Siluriformes
Ergasilus tipurus Varella, Morey & Malta, 2019	–	–	X	–	–	–	–	–	Characiformes; Siluriformes
Ergasilus tissensis D'yachenko, 1969	X	–	–	–	–	–	–	–	Cypriniformes
Ergasilus triangularis Malta, 1996	–	–	X	–	–	–	–	–	Characiformes
Ergasilus trygonophilus Domingues & Marques, 2010	–	–	X	–	–	–	–	–	Myliobatiformes
Ergasilus tumidus Markevich, 1940	X	–	–	–	X	–	–	–	Cypriniformes
Ergasilus turgidus Fraser, 1920	–	X	–	–	X	–	–	–	Cypriniformes; Ovalentaria/misc; Perciformes/Gasterosteoidei; Salmoniformes
Ergasilus turkayi Marques, Clebsh, Cordova & Boeger, 2017	–	–	X	–	–	–	–	–	Characiformes
Ergasilus turucuyus Malta & Varella, 1996	–	–	X	–	–	–	–	–	Characiformes
Ergasilus uniseriatus Ho, Jayarajan & Radhakrishnan, 1992	–	–	–	–	X	–	–	–	Beloniformes; Gobiiformes
Ergasilus urupaensis Malta, 1995	–	–	X	–	–	–	–	–	Characiformes
Ergasilus vembanadensis Thomas S., 1993	–	–	–	–	X	–	–	–	Siluriformes
Ergasilus ventriosus Kim I.H. & Choi, 2003	X	–	–	–	–	–	–	–	Cypriniformes
Ergasilus versicolor Wilson C.B., 1911 (= *Ergasilus elegans* Wilson, C.B., 1916)	–	X	X	–	–	–	–	–	Anguilliformes; Centrarchiformes; Cypriniformes; Eupercaria/misc; Lepisosteiformes; Mugiliformes; Perciformes/Gasterosteoidei; Siluriformes

Species	PA	NA	NT	AT	OL	AU	PAC	ANT	Hosts
Ergasilus wareaglei Johnson S.K., 1973	–	X	–	–	–	–	–	–	Cypriniformes
Ergasilus wilsoni Markevich, 1933	X	–	–	–	–	–	–	–	Clupeiformes; Cypriniformes; Gobiiformes; Osmeriformes; Perciformes/Cottoidei; Perciformes/Gasterosteoidei; Pleuronectiformes; Salmoniformes
Ergasilus xenomelanirisi Carvalho, 1955	–	–	X	–	–	–	–	–	Atheriniformes
Ergasilus xinguensis Taborda, Paschoal & Luque, 2016	–	–	X	–	–	–	–	–	Characiformes; Cichliformes; Eupercaria/misc; Siluriformes
Ergasilus xinjiangensis Kuang & Qian, 1985	X	–	–	–	–	–	–	–	Cypriniformes
Ergasilus yaluzangbus Kuang & Qian, 1985	X	–	–	–	–	–	–	–	Cypriniformes
Ergasilus yandemontei Waicheim, Mendes Marques, Rauque & Viozzi, 2021	–	–	X	–	–	–	–	–	Atheriniformes; Centrarchiformes; Galaxiiformes
Ergasilus youngi Tavares & Luque, 2005	–	–	X	–	–	–	–	–	Siluriformes
Ergasilus yumaricus Malta & Varella, 1995	–	–	X	–	–	–	–	–	Characiformes
Ergasilus zacconis (Yamaguti, 1936) (= *Pseudergasilus zacconis* Yamaguti, 1936)	X	–	–	–	–	–	–	–	Cypriniformes; Osmeriformes
Gamidactylus bryconis Varella, 1995	–	–	X	–	–	–	–	–	Characiformes
Gamidactylus hoplius Varella & Malta, 1996	–	–	X	–	–	–	–	–	Characiformes
Gamidactylus jaraquensis Thatcher & Boeger, 1984	–	–	X	–	–	–	–	–	Characiformes
Gamidactylus piranhus Thatcher, Santos & Brasil-Sato, 2008	–	–	X	–	–	–	–	–	Characiformes
Gamispatulus ferrilongus Narciso & Silva, 2020	–	–	X	–	–	–	–	–	Characiformes
Gamispatulus schizodontis Thatcher & Boeger, 1984	–	–	X	–	–	–	–	–	Characiformes
Gamispinus diabolicus Thatcher & Boeger, 1984	–	–	X	–	–	–	–	–	Siluriformes
Gauchergasilus euripedesi (Montú, 1980) (= *Ergasilus euripedesi* Montú, 1980)	–	–	X	–	–	–	–	–	Cichliformes, Clupeiformes, Characiformes, Eupercaria/misc, Gobiesociformes, plankton
Majalincola buthi Tang & Kalman, 2008	–	–	–	–	–	X	–	–	Tetraodontiformes
Miracetyma etimaruya Malta, 1993	–	–	X	–	–	–	–	–	Characiformes
Miracetyma kawa Malta, 1994	–	–	X	–	–	–	–	–	Characiformes
Miracetyma piraya Malta, 1993	–	–	X	–	–	–	–	–	Characiformes
Mugilicola australiensis Boxshall, 1986	–	–	–	–	–	X	–	–	Eupercaria/misc (Sillaginidae)
Mugilicola bulbosa Tripathi, 1960 (= *Paeonodes mugilis* Pillai & Jayasree, 1978)	X	–	–	–	X	–	–	–	Mugiliformes
Mugilicola kabatai Piasecki, Khamees & Mhaisen, 1991	X	–	–	–	–	–	–	–	Mugiliformes
Mugilicola smithae Jones J.B. & Hine, 1978	–	–	–	X	–	–	–	–	Anguilliformes, Mugiliformes, Myxiniformes
Neoergasilus africanus Fikiye, Van As, Truter, Smit & Hadfield, 2024	–	–	–	X	–	–	–	–	Siluriformes
Neoergasilus angustus Kim I.H. & Choi, 2003	X	–	–	–	–	–	–	–	Centrarchiformes, Cypriniformes
Neoergasilus bullatus Kim I.H. & Choi, 2003	X	–	–	–	–	–	–	–	Cypriniformes
Neoergasilus ferozepurensis Kumari, Khera & Gupta, 1988	–	–	–	–	X	–	–	–	Beloniformes

Species	PA	NA	NT	AT	OL	AU	PAC	ANT	Hosts
Neoergasilus indicus Vankara & Chikkam, 2010	–	–	–	–	X	–	–	–	Synbranchiformes
Neoergasilus japonicus (Harada, 1930) (= *Ergasilus japonicus* Harada, 1930)	X	X	X	X	X	–	–	–	Anabantiformes, Beloniformes, Centrarchiformes, Characiformes, Cichliformes, Cyprinodontiformes, Cypriniformes, Esociformes, Gadiformes, Gobiiformes, Mugiliformes, Ovalentaria/misc (Ambassidae), Perciformes, Salmoniformes, Siluriformes
Neoergasilus kherai Batish & Brar, 1989	–	–	–	–	X	–	–	–	Cypriniformes
Neoergasilus longispinosus Yin, 1956	X	–	–	–	X	–	–	–	Clupeiformes, Cypriniformes
Neoergasilus notopteri Kumari, Khera & Gupta, 1988	–	–	–	–	X	–	–	–	Osteoglossiformes
Neoergasilus spinipes (Byrnes, 1986) (= *Ergasilus spinipes*, Byrnes 1986)	–	–	–	–	–	X	–	–	Eupercaria/misc (Sparidae)
Neoergasilus squaliobarbi (Dogiel & Akhmerov, 1952) (= *Ergasilus squaliobarbi* Dogiel & Akhmerov, 1952; *Neoergasilus inflatus* Yin, 1956)	X	–	–	–	X	–	–	–	Anabantiformes, Centrarchiformes, Cypriniformes, Siluriformes, Synbranchiformes
Nipergasilus bora (Yamaguti, 1939) (= *Ergasiloides bora* Yamaguti, 1939; *Yamagutia bora* (Yamaguti, 1939)	X	–	–	X	X	–	–	–	Mugiliformes
Nipergasilus parabora El-Rashidy & Boxshall, 2000	–	–	–	–	X	–	–	–	Mugiliformes
Paeonodes exiguus Wilson C.B., 1944	–	X	–	–	–	–	–	–	unverified (“Verilida grayula”, Lutjanidae?)
Paeonodes lagunaris Banning, 1974	–	–	–	X	–	–	–	–	Cichliformes
Paeonodes nemaformis Hewitt, 1969	–	–	–	–	–	X	–	–	Salmoniformes
Paeonodes subviridis El-Rashidy & Boxshall, 2001	–	–	–	–	–	–	X	–	Mugiliformes
Paraergasilus acanthopagri Roubal, 1981	–	–	–	–	–	X	–	–	Eupercaria/misc (Sparidae)
Paraergasilus brevidigitus Yin, 1954	X	–	–	–	X	–	–	–	Acipenseriformes, Cypriniformes, Siluriformes, plankton
Paraergasilus curtus El-Rashidy & Boxshall, 2001	–	–	–	X	X	X	–	–	Mugiliformes
Paraergasilus dentatus Ho, Jayarajan & Radhakrishnan, 1992	X	–	–	–	X	–	–	–	Gobiiformes
Paraergasilus dichotomus El-Rashidy & Boxshall, 2001	–	–	–	–	–	X	–	–	Mugiliformes
Paraergasilus inflatus Ho, Khamees & Mhaisen, 1996	X	–	–	–	–	–	–	–	Cypriniformes, Mugiliformes, Siluriformes
Paraergasilus lagoonaris Paperna, 1969	–	–	–	X	–	–	–	–	Cichliformes, Clupeiformes, Cyprinodontiformes, Gobiiformes
Paraergasilus longidigitus Yin, 1954 (= *Paraergasilus rylovi boristhenicus* Sukhenko, 1967)	X	X	–	–	X	–	–	–	Acropomatiformes, Anabantiformes, Centrarchiformes, Cypriniformes, Esociformes, Eupercaria/misc (Sparidae), Perciformes/Percoidei, Siluriformes
Paraergasilus medius Yin, 1956	X	–	–	–	X	–	–	–	Cypriniformes, Esociformes
Paraergasilus mimus Yin, 1962	X	–	–	–	–	–	–	–	Siluriformes
Paraergasilus minutus (Fryer, 1956)	–	–	–	X	–	–	–	–	Cichliformes

Species	PA	NA	NT	AT	OL	AU	PAC	ANT	Hosts
(= *Trigasilus minutus* Fryer, 1956)									
Paraergasilus platyhoraxis Liu & Wang, 1997	–	–	–	–	X	–	–	–	Cypriniformes
Paraergasilus reductus Ranga Reddy & Kasaiah, 1994	–	–	–	–	X	–	–	–	plankton
Paraergasilus remulus Cressey, in Cressey & Collette, 1970	–	–	–	–	X	–	–	–	Beloniformes
Paraergasilus rylovi Markevich, 1937 (= *Paraergasilus markevichi* Titar & Chernogorenko, 1982)	X	–	–	–	–	–	–	–	Acipenseriformes, Cypriniformes, Gobiiformes, Perciformes/Percoidei, Siluriformes, Bivalvia, plankton
Pindapixara tarira Malta, 1995	–	–	X	–	–	–	–	–	Characiformes
Prehendorastrus bidentatus Boeger & Thatcher, 1990	–	–	X	–	–	–	–	–	Siluriformes
Prehendorastrus monodontus Boeger & Thatcher, 1990	–	–	X	–	–	–	–	–	Siluriformes
Pseudovaigamus spinicephalus (Thatcher & Robertson B.A., 1984) (= *Vaigamus spinicephalus* Thatcher & Robertson B.A., 1984; *Ergasilus spinicephalus* (Thatcher & Robertson B.A., 1984))	–	–	X	–	–	–	–	–	plankton
Pseudovaigamus tridentatus Narciso, Perbiche-Neves & Silva, 2020	–	–	X	–	–	–	–	–	Siluriformes
Rhinergasilus digitus Narciso, Brandao, Perbiche-Neves & Silva, 2020	–	–	X	–	–	–	–	–	Characiformes
Rhinergasilus piranhus Boeger & Thatcher, 1988	–	–	X	–	–	–	–	–	Characiformes, Cichliformes
Rhinergasilus unguilongus Narciso, Perbiche-Neves & Silva, 2021	–	–	X	–	–	–	–	–	Characiformes
Sinergasilus major (Markevich, 1940) (= *Pseudergasilus major* Markevich, 1940; *Sinergasilus yuii* Yin, 1949)	X	–	–	–	X	–	–	–	Acanthuriformes, Centrarchiformes, Cichliformes, Cypriniformes, Gobiiformes, Mugiliformes, Perciformes/Percoidei, Salmoniformes, Siluriformes
Sinergasilus polycolpus (Markevich, 1940) (= *Pseudergasilus polycolpus* Markevich, 1940; *Sinergasilus lieni* Yin, 1949)	X	–	–	–	X	–	–	–	Cypriniformes
Sinergasilus undulatus (Markevich, 1940) (= *Pseudergasilus undulatus* Markevich, 1940)	X	–	–	–	X	–	–	–	Centrarchiformes, Cypriniformes
Teredophilus inflatus (Harding, 1964) (= *Ergasiluxulus inflatus* Harding, 1964)	–	–	–	X	–	–	–	–	Bivalvia
Teredophilus renicola Rancurel, 1954	–	–	–	X	–	–	–	–	Bivalvia
Therodamas dawsoni Cressey, 1972	–	–	X	–	–	–	–	–	Blenniiformes
Therodamas elongatus (Thatcher, 1986) (= *Amazonicopeus elongatus* Thatcher, 1986; *Therodamas tamarae* Amado & Rocha C.E.F., 1996)	–	–	X	–	–	–	–	–	Eupercaria/misc (Sciaenidae)
Therodamas fluviatilis Paggi, 1977	–	–	X	–	–	–	–	–	Characiformes, Pleuronectiformes
Therodamas frontalis El-Rashidy & Boxshall, 2001	–	–	X	–	–	–	–	–	Mugiliformes, Siluriformes
Therodamas longicollum Oliveira, Correa, Adriano & Tavares-Dias, 2021	–	–	X	–	–	–	–	–	Characiformes

Species	PA	NA	NT	AT	OL	AU	PAC	ANT	Hosts
Therodamas mexicanus Suárez-Morales, Santana-Pineros & González-Solís, 2008	–	–	X	–	–	–	–	–	Carangaria/misc (Carangiformes)
Therodamas serrani Krøyer, 1863	–	–	X	–	–	–	–	–	Perciformes/Serranoidei, plankton
Therodamas sphyricephalus Thomsen, 1949	–	–	X	–	–	–	–	–	Siluriformes
Thersitina gasterostei (Pagenstecher, 1861) (= *Thersites gasterostei* Pagenstecher, 1861; *Ergasilus gasterostei* (Pagenstecher, 1861); *Ergasilus biuncinatus* Gadd, 1901; *Thersitina biuncinata* (Gadd, 1901); *Limnoncaea diuncata* Kokubo, 1914)	X	X	–	–	–	–	–	–	Atheriniformes, Cypriniformes, Gobiiformes, Perciformes/Gasterosteoidei, Osmeriformes, Perciformes/Percoidei, Syngnathiformes
Thersitina kasaharai (Do, 1981) (= *Diergasilus kasaharai* Do, 1981)	X	–	–	–	X	–	–	–	Gonorynchiformes, Mugiliformes, Osmeriformes
Tiddergasilus bipartitus Narciso, Vieira & Silva, 2022	–	–	X	–	–	–	–	–	Characiformes
Tiddergasilus iheringi (Tidd, 1942) (= *Ergasilus iheringi* Tidd, 1942)	–	–	X	–	–	–	–	–	Characiformes
Urogasilus brasiliensis Rosim, Boxshall & Ceccarelli, 2013	–	–	X	–	–	–	–	–	Characiformes, Cichliformes
Vaigamus retrobarbatus Thatcher & Robertson B.A., 1984 (= *Ergasilus retrobarbatus* Thatcher & Robertson B.A., 1984)	–	–	X	–	–	–	–	–	plankton

Supplementary Table 2 Checklist of all valid species of Lernaeidae, including recognised synonyms, with their documented distribution across biogeographical regions and known host associations.

Species	PA	NA	NT	AT	OL	AU	PAC	ANT	Hosts
***Lamprogleninae* Sproston, Yin & Hu, 1950**									
Afrolernaea annemari Oldewage, 1994	–	–	–	X	–	–	–	–	Siluriformes
Afrolernaea brevicollis Fryer, 1982	–	–	–	X	–	–	–	–	Osteoglossiformes
Afrolernaea edi Oldewage, 1994	–	–	–	X	–	–	–	–	Osteoglossiformes
Afrolernaea longicollis Fryer, 1956	–	–	–	X	–	–	–	–	Osteoglossiformes
Afrolernaea mormyroides Van As, 1983	–	–	–	X	–	–	–	–	Osteoglossiformes
Afrolernaea nigeriensis (Dollfus, 1960) (= *Delamarina nigeriensis* Dollfus, 1960)	–	–	–	X	–	–	–	–	Osteoglossiformes
Catlaphilla elongata Tripathi, 1960	–	–	–	–	X	–	–	–	Cypriniformes
Catlaphilla lingi Manohar, Seenappa, Venkateshappa & Shetty, 1981	–	–	–	–	X	–	–	–	Cypriniformes
Indolernaea gurayai (Battish & Brar, 1989) (= *Lamproglena gurayai* Battish & Brar, 1989)	–	–	–	–	X	–	–	–	Siluriformes
Indolernaea macronii (Manohar, Venkateshappa & Seenappa, 1991) (= *Pseudolernaea macronii* Manohar, Venkateshappa & Seenappa, 1991)	–	–	–	–	X	–	–	–	Siluriformes
Indolernaea manohari Kabata, 1983	–	–	–	–	X	–	–	–	Siluriformes
Indolernaea seenghalae (Kumari, Khera & Gupta, 1989) (= *Lamproglena seenghalae* Kumari, Khera & Gupta, 1989)	–	–	–	–	X	–	–	–	Siluriformes
Indopeniculus fryeri Kumari, Khera & Gupta, 1988	–	–	–	–	X	–	–	–	Osteoglossiformes
Indopeniculus siamensis Ho & Kim I.H., 1997	–	–	–	–	X	–	–	–	unknown
Lamproglena angusta Wilson, 1924	–	–	–	X	–	–	–	–	Siluriformes
Lamproglena barbicola Fryer, 1961	–	–	–	X	–	–	–	–	Cypriniformes
Lamproglena brevis Kuang, 1977	–	–	–	–	X	–	–	–	Cypriniformes
Lamproglena carassii Sproston, Yin & Hu, 1950	X	–	–	–	X	–	–	–	Cypriniformes
Lamproglena cavasii Kumari, Khera & Gupta, 1989	–	–	–	–	X	–	–	–	Cypriniformes, Siluriformes
Lamproglena chinensis Yü, 1937 (= *Lamproglena chinensis sprostoni* Kirtisinghe, 1964)	X	–	–	–	X	–	–	–	Anabantiformes, Cypriniformes, Scombriformes, Siluriformes
Lamproglena cirrhinae Kuang & Qian, 1985	X	–	–	–	X	–	–	–	Cypriniformes
Lamproglena clariae Fryer, 1956	–	–	–	X	–	–	–	–	Siluriformes

Species	PA	NA	NT	AT	OL	AU	PAC	ANT	Hosts
Lamproglena cleopatra Humes, 1957	–	–	–	X	–	–	–	–	Cypriniformes
Lamproglena compacta Markevich, 1936	X	–	–	–	–	–	–	–	Cypriniformes, Siluriformes
Lamproglena cornuta Fryer, 1965	–	–	–	X	–	–	–	–	Siluriformes
Lamproglena curta Gusev, 1950	X	–	–	–	X	–	–	–	Cypriniformes
Lamproglena cylindrata Kuang, 1977	–	–	–	–	X	–	–	–	Cypriniformes
Lamproglena dibara Kuang, 1991	–	–	–	–	X	–	–	–	Cypriniformes
Lamproglena elongata Capart, 1956	–	–	–	X	–	–	–	–	Characiformes
Lamproglena forficata Kuang, 1977	–	–	–	–	X	–	–	–	Anabantiformes
Lamproglena hemprichii von Nordmann, 1832 (= *Lamproglena aubentoni* Dollfus, 1960)	–	–	–	X	–	–	–	–	Characiformes
Lamproglena hepseti Van As & Van As, 2007	–	–	–	X	–	–	–	–	Characiformes
Lamproglena heterognatha Kuang & Qian, 1985	–	–	–	–	X	–	–	–	Cypriniformes
Lamproglena hoi Dippenaar, Luus-Powell & Roux, 2001	–	–	–	X	–	–	–	–	Cypriniformes
Lamproglena hospetensis Manohar, Seenappa & Venkateshappa, 1992	–	–	–	–	X	–	–	–	Siluriformes
Lamproglena indica Kumari, Khera & Gupta, 1989	–	–	–	–	X	–	–	–	Siluriformes
Lamproglena inermis Capart, 1943	–	–	–	–	X	–	–	–	Cypriniformes, Osteoglossiformes
Lamproglena intercedens Fryer, 1964	–	–	–	X	–	–	–	–	Characiformes
Lamproglena jordani Paperna, 1964	X	–	–	–	–	–	–	–	Cypriniformes
Lamproglena krishnai Thomas & Hameed, 1984	–	–	–	–	X	–	–	–	Anabantiformes
Lamproglena lichiae von Nordmann, 1832	–	–	–	X	–	–	–	–	Carangiformes
Lamproglena markewitschi Sukhenko & Allamuratov, 1966	X	–	–	–	–	–	–	–	Cypriniformes
Lamproglena meridiona Kuang & Qian, 1985	–	–	–	–	X	–	–	–	Cypriniformes
Lamproglena minuta Capart, 1943	–	–	–	–	X	–	–	–	Cypriniformes
Lamproglena mongtinensis Kuang, 1977	–	–	–	–	X	–	–	–	Cypriniformes
Lamproglena monodi Capart, 1944 (= *Lamproglena nyasae* Fryer, 1956)	–	–	X	X	–	–	–	–	Cichliformes
Lamproglena notopterai Jafri & Mahar, 2006	–	–	–	–	X	–	–	–	Osteoglossiformes
Lamproglena orientalis Markevich, 1936 (= *Lamproglena ophiocephali* Yamaguti, 1939)	X	–	–	–	X	–	–	–	Cypriniformes
Lamproglena pulchella von Nordmann, 1832	X	–	–	–	–	–	–	–	Cypriniformes, Esociformes, Mugiliformes
Lamproglena robusta Capart, 1943	–	–	–	–	X	–	–	–	Siluriformes
Lamproglena semilabecola Liu & Wang, 1997	–	–	–	–	X	–	–	–	Cypriniformes
Lamproglena werneri Zimmermann, 1923	–	–	–	X	–	–	–	–	Siluriformes
Lamproglena wilsoni Capart, 1955	–	–	–	X	–	–	–	–	Siluriformes
Lamproglena yunnanensis Kuang, 1977	–	–	–	–	X	–	–	–	Cypriniformes
Lamproglenoides floricapitis Kuang, 1979	–	–	–	–	X	–	–	–	Cypriniformes

Species	PA	NA	NT	AT	OL	AU	PAC	ANT	Hosts
Lamproglenoides vermifornis Fryer, 1964	–	–	–	X	–	–	–	–	Cypriniformes
Pseudolamproglena annulata Boxshall, 1976	X	–	–	–	–	–	–	–	Cypriniformes
Pseudolamproglena boxshalli Al-Naisri, Ho & Mhaisen, 2012	X	–	–	–	–	–	–	–	Cypriniformes
Pseudolamproglena simplex Boxshall, 1976	–	–	–	–	X	–	–	–	Cypriniformes
Pseudolamproglena sinilabis (Kuang, 1980) (= *Mesolamproglena sinilabis* Kuang, 1980)	–	–	–	–	X	–	–	–	Cypriniformes
Pseudolamproglena zahrziensis Míč & Seifertová, 2025	X	–	–	–	–	–	–	–	Cypriniformes
Lernaeinae Wilson C.B., 1917									
Amazolernaea sannerae Thatcher & Williams, 1998	–	–	X	–	–	–	–	–	Cichliformes
Areotrachelus truchae (Brian, 1903) (= *Silvestria truchae* Brian, 1903; *Leptotrachelus truchae* Brian, 1903)	–	–	X	–	–	–	–	–	Centrarchiformes
Bedsylernaea collaris Thatcher & Williams, 1998	–	–	X	–	–	–	–	–	Characiformes
Dysphorus torquatus Kurtz, 1924	–	–	–	X	–	–	–	–	Osteoglossiformes
Lernaea arcuata Soejanto, 1965	–	–	–	–	X	–	–	–	Cypriniformes
Lernaea argentinensis Paggi, 1972	–	–	X	–	–	–	–	–	Characiformes, Siluriformes
Lernaea bagri Harding, 1950	–	–	–	X	–	–	–	–	Siluriformes
Lernaea barbicola Leigh-Sharpe, 1930	–	–	–	X	–	–	–	–	Cypriniformes
Lernaea barilii Harding, 1950	X	–	–	X	–	–	–	–	Cypriniformes
Lernaea barnimiana (Hartmann, 1865) (= *Lernaeocera barnimiana* Hartmann, 1865; *Lernaeocera barnimii* Hartmann, 1870; *Lernaea barnimii* (Hartmann, 1970); *Lernaeocera temnocephala* Cunnington, 1914; *Lernaea temnocephala* (Cunnington, 1914)	–	–	–	X	–	–	–	–	Carangaria/misc (Latidae), Cichliformes, Cypriniformes
Lernaea bengalensis Gnanamuthu, 1951	–	–	–	–	X	–	–	–	Anabantiformes
Lernaea bhadraensis Seenappa, Manohar & Shetty, 1980	–	–	–	–	X	–	–	–	Cypriniformes
Lernaea bistricornis Harding, 1950	–	–	–	X	–	–	–	–	Cichliformes
Lernaea catostomi (Krøyer, 1863) (= *Lernaeocera catostomi* Krøyer, 1863; *Lernaeocera tortua* Kellicott, 1881; *Lernaea tortua* (Kellicott, 1881); *Lernaeocera pectoralis* Kellicott, 1882)	–	X	–	–	–	–	–	–	Cypriniformes, Siluriformes
Lernaea composita Wilson C.B., 1924	–	–	–	X	–	–	–	–	Characiformes, Polypteriformes, Siluriformes
Lernaea cruciata (Le Sueur, 1824) (= *Lernaeocera cruciata* Le Sueur, 1824)	–	X	–	–	X	–	–	–	Centrarchiformes, Cypriniformes, Cyprinodontiformes, Eupercaria/misc (Moronidae), Osteoglossiformes
Lernaea ctenopharyngodontis Yin, 1960	X	–	–	–	X	–	–	–	Cypriniformes

Species	PA	NA	NT	AT	OL	AU	PAC	ANT	Hosts
Lernaea cyprinacea Linnaeus, 1758 (= *Lernaea tentaculis quatuor* Linnaeus, 1746; *Lernaea tentaculis* Linnaeus, 1746; *Lernaeocera cyprinata* (Linnaeus, 1746); *Lernaeocera gasterostei* Brühl, 1860; *Lernaea elegans* Leigh-Sharpe, 1925; *Lernaea ranae* Stunkard & Cable, 1931; *Lernaea carassii* Tidd, 1933; *Lernaea cyprinacea brachycera* (Yü, 1938); *Lernaea cyprinacea chakoensis* (Gnanamuthu, 1951); *Lernaea cyprinacea cyprinacea* Linnaeus, 1758; *Lernaea cyprinacea elegans* Leigh-Sharpe, 1925; *Lernaea cyprinacea macropodi* Hu, 1948; *Lernaea cyprinacea mastacembeli* Hu, 1948)	X	X	X	X	X	X	–	–	Acipenseriformes, Amiiformes, Anabantiformes, Anguilliformes, Anura (Amphibia), Atheriniformes, Blenniiformes, Centrarchiformes, Characiformes, Cichliformes, Clupeiformes, Cypriniformes, Cyprinodontiformes, Esociformes, Eupercaria/misc, Gadiformes, Gasterosteiformes, Gobiiformes, Mugiliformes, Osmeriformes, Osteoglossiformes, Perciformes, Salmoniformes, Scorpaeniformes, Scombriformes, Siluriformes, Synbranchiformes
Lernaea devastatrix Boxshall, Montú & Schwarzbold, 1997	–	–	X	–	–	–	–	–	Characiformes, Cypriniformes, Siluriformes
Lernaea diceracephala (Cunnington, 1914) (= *Lernaeocera diceracephala* Cunnington, 1914)	–	–	–	X	–	–	–	–	Siluriformes
Lernaea dolabrodes Wilson C.B., 1917	–	X	–	–	–	–	–	–	Centrarchiformes
Lernaea gambusiae Koul & Raina, 1990	–	–	–	–	X	–	–	–	Cyprinodontiformes
Lernaea gonionoti Kularatne, 1993	–	–	–	–	X	–	–	–	Cypriniformes
Lernaea haplocephala (Cunnington, 1914) (= *Lernaeocera haplocephala* Cunnington, 1914; *Lernaeocera bichiri* Kurtz, 1922; *Lernaea bichiri* (Kurtz, 1922))	–	–	–	X	–	–	–	–	Polypteriformes
Lernaea hardingi Fryer, 1956	–	–	–	X	–	–	–	–	Characiformes, Cichliformes, Siluriformes
Lernaea hesaragattensis Srinivasachar & Sundarabai, 1971	–	–	–	–	X	–	–	–	Cyprinodontiformes
Lernaea inflata Fryer, 1961	–	–	–	X	–	–	–	–	Cypriniformes
Lernaea insolens Wilson C.B., 1919	–	X	–	–	–	–	–	–	Centrarchiformes
Lernaea kashmirensis Malhotra & Jyoti, 1972	–	–	–	–	X	–	–	–	Cypriniformes
Lernaea kuangi (Kuang, in Kuang & Qian, 1983) (= *Lernaea minuta* Kuang, in Kuang & Qian, 1983)	–	–	–	–	X	–	–	–	Cypriniformes
Lernaea lagenula (Heller, 1865) (= *Lernaeocera lagenula* Heller, 1865)	–	–	X	–	–	–	–	–	unknown
Lernaea lophiara Harding, 1950	–	–	–	X	X	–	–	–	Cichliformes, Cypriniformes, Cyprinodontiformes, Siluriformes
Lernaea minima Otte, 1965	X	–	–	–	–	–	–	–	Salmoniformes
Lernaea multiobosa Jafri & Mahar, 2003	–	–	–	–	X	–	–	–	Cypriniformes
Lernaea octocornua Yin, 1960	–	–	–	–	X	–	–	–	Anabantiformes
Lernaea oryzophila Monod, 1932	X	–	–	–	X	–	–	–	Cypriniformes, Gobiiformes
Lernaea osphronemi Thomas & Hameed, 1988	–	–	–	–	X	–	–	–	Anabantiformes
Lernaea palati Harding, 1950	–	–	–	X	–	–	–	–	Cichliformes
Lernaea papuensis Boxshall, 1981	–	–	–	–	–	X	–	–	Osteoglossiformes

Species	PA	NA	NT	AT	OL	AU	PAC	ANT	Hosts
Lernaea parasiluri Yü, 1938	X	–	–	–	X	–	–	–	Siluriformes
Lernaea phoxinacea (Krøyer, 1863) (= *Lernaeocera phoxinacea* Krøyer, 1863)	X	–	–	–	–	–	–	–	Cypriniformes
Lernaea piscinae Harding, 1950	–	–	–	–	X	–	–	–	Cypriniformes
Lernaea polymorpha Yü, 1938	–	–	–	–	X	–	–	–	Cypriniformes
Lernaea pomotidis (Krøyer, 1863) (= *Lernaeocera pomotidis* Krøyer, 1863)	–	X	–	–	–	–	–	–	Centrarchiformes, Siluriformes
Lernaea quadrinucifera Yin, 1960	–	–	–	–	X	–	–	–	Cypriniformes
Lernaea rhodei Hu, 1948	–	–	–	–	X	–	–	–	Cypriniformes
Lernaea senegali (Zimmermann, 1922) (= *Lernaeocera senegali* Zimmermann, 1922)	–	–	–	X	–	–	–	–	Polypteriformes
Lernaea taipila Ho & Kim I.H., 1997	–	–	–	–	X	–	–	–	Cichliformes
Lernaea tenuis (Wilson C.B., 1916) (= *Lernaeocera tenuis* Wilson C.B., 1916)	–	X	–	–	–	–	–	–	Eupercaria/misc (Sciaenidae)
Lernaea tilapiae Harding, 1950	–	–	–	X	–	–	–	–	Cichliformes
Lernaea tuberosa Harding, 1950	–	–	–	X	–	–	–	–	Cypriniformes
Lernaea variabilis (Wilson C.B., 1916) (= *Lernaeocera variabilis* Wilson C.B., 1916)	–	X	–	–	–	–	–	–	Centrarchiformes, Lepisosteiformes, Perciformes/Percoidei, Siluriformes
Lernaeogiraffa heterotidicola Zimmermann, 1922	–	–	–	X	–	–	–	–	Osteoglossiformes
Minilernaea floricapitella Thatcher & Huergo, 2005	–	–	X	–	–	–	–	–	Characiformes, Siluriformes
Opistholernaea contorta Fryer, 1965	–	–	–	X	–	–	–	–	Characiformes
Opistholernaea giganticauda Yin, 1960	–	–	–	–	X	–	–	–	Anabantiformes
Opistholernaea laterobrachialis (Fryer, 1959) (= *Opistholernaea laterobrachialis nitotica* Fryer, 1965)	–	–	–	X	–	–	–	–	Cichliformes
Opistholernaea longa (Harding, 1950)	–	–	–	X	–	–	–	–	Carangaria/misc (Latidae)
Perulernaea gamitanae Thatcher & Paredes, 1985	–	–	X	–	–	–	–	–	Characiformes
Perulernaea pirapitingae Thatcher, 2000	–	–	X	–	–	–	–	–	Characiformes
Pillainus neculatus (Kumari, Gupta & Khera, 1987) (= *Channaculina neculatus* Kumari, Gupta & Khera, 1987)	–	–	–	–	X	–	–	–	Anabantiformes
Pillainus volvicollis Kabata, 1983	–	–	–	–	X	–	–	–	Anabantiformes

Note: The Palearctic–Oriental boundary in southern China is difficult to define because the transition between temperate and subtropical zones is gradual and many Chinese records lack precise geographic coordinates, often listing only counties or large regional names. This vagueness complicates biogeographic assignment, but several southern Chinese localities clearly fall within the Oriental region. These include Lianjiang County in Guangdong, Baisha in Jiangyou County in Sichuan, multiple sites in Yunnan such as Mengding and Baoshan, localities in Guizhou such as Songtao and Yinjiang, and all records from Hainan Island, which is entirely Oriental in biogeographic affinity.

Notes on excluded taxa and nomenclatural issues

Several taxa reported in the literature were excluded from the global checklist of Ergasilidae and Lernaeidae because their identities are uncertain, their original descriptions are inadequate, or their taxonomic placement cannot be evaluated with confidence.

The genus *Anklobrachius* Thatcher, 1999 was not incorporated into the framework of Ergasilidae. The genus was erected solely on the basis of male specimens, whereas ergasilid systematics rely almost entirely on female morphology. Male antennal and antennulary structures are strongly sexually dimorphic and do not provide a reliable basis for generic diagnosis. *Anklobrachius* is therefore treated as a *genus inquirendum* following Boxshall & Halsey (2004).

The historical genera *Macrobrachinus* Hesse, 1871 and *Megabrachinus* Hesse, 1871 are likewise treated as *genera inquirenda*, as the available material and descriptions are insufficient to assess their affinities. The species *Megabrachinus suboculatus* Hesse, 1871 is treated as *Ergasilus suboculatus* (Hesse, 1871) following current usage in WoRMS and is counted under that name in the checklist.

The nomenclature of *Sinergasilus polycolpus* has been historically inconsistent. The genus *Sinergasilus* was erected by Yin (1949) for *S. lieni* and *S. yuii*, based on material from Chinese pond systems, and was distinguished from *Pseudergasilus* by trunk morphology, reduction of leg 5 and mouthpart structure. Yin (1956) subsequently transferred *Pseudergasilus major* and *P. undulatus* to *Sinergasilus* and treated *P. polycolpus* as conspecific with *S. lieni*, while also reinterpreting *S. yuii* as a junior synonym of *S. major*. This revision established the modern concept of three species within the genus but introduced ambiguity regarding the correct name. Russian and Chinese authors continued to use *S. lieni* in subsequent works (Bykhovskaya-Pavlovskaya *et al*., 1962, 1964), whereas later Chinese and European literature increasingly adopted *S. polycolpus* on the basis of priority (e.g. Wang *et al*., 2002; Cakić *et al*., 2004; Blažeković-Dimovska & Stojanovski, 2015). Mixed usage persists in parts of the recent literature (e.g. Molnár & Székely, 2004; Nitta & Nagasawa, 2020; Yevtushenko, 2020). Under the Principle of Priority of the International Code of Zoological Nomenclature, *Sinergasilus polycolpus* Markevich, 1940 is the valid name and is adopted here.

Thersitina inopinata Percival, 1937 was excluded because it was described solely from a free-swimming male with atypical morphology. The construction of leg 4, consisting of a one-segmented unarmed exopod combined with a two-segmented endopod, is incompatible with

the diagnosis of *Thersitina* and atypical for Ergasilidae. The species is therefore regarded as *incertae sedis* and is not treated as a valid ergasilid taxon (Ohtsuka *et al*., 2004).

Within Lernaeidae, *Lamproglena intercedens* Fryer, 1964 is retained as a valid species. Claims that it was transferred to *Catlaphilla* by Ho (1998) in Dippenaar *et al*. (2001) and Kunutu *et al*. (2018) are unsupported and do not correspond to any published taxonomic action. No subsequent revision has provided evidence for such a reassignment.

Lamproglena notopterai Jafri & Mahar, 2006 is provisionally maintained as valid. Although the description is imprecise in parts, the published illustrations clearly depict a female specimen with a consistent diagnostic character set. The species is retained pending further material and critical revision.

Subspecific names within *Lamproglena chinensis* and *Lernaea cyprinacea* are not recognised in the present study and are treated within their respective nominal species.

The following nominal species of *Lernaea* are excluded from the checklist because their identities are uncertain or their original descriptions are inadequate for reliable diagnosis: *Lernaea basteri* Blainville, 1822; *Lernaea gadniminuti* Hesse, 1870; *Lernaea lotae* Hermann, 1783; *Lernaea marionis* Blainville, 1822; *Lernaea multicornis* Cuvier, 1830; *Lernaea sieboldi* Koch, 1860; and *Lernaea squamicola* Hermann, 1783.

Several names assigned to *Catlaphilla* in regional checklists lack verifiable hosts, precise localities, accessible original descriptions, or compliance with modern nomenclatural standards. These include *Catlaphilla bhagirathiae* Battish, 1981; *Catlaphilla eurynotus* Sars; *Catlaphilla horrida* Vavra, 1985; *Catlaphilla parvus parvus* Calus, 1863; and *Catlaphilla rohitae* Kumari, 1985. All are treated here as *nomina dubia* and are excluded from the checklist.

Paper 5 (submitted manuscript in Acta Parasitologica)

Adday, T. K., Ali, A. H., & **Míč R.** (2026). Description of a new species of *Dermoergasilus planilizai* sp. nov. (Copepoda: Ergasilidae) from abu mullet *Planiliza abu* (Heckel) gills at the Al-Gharraf River, Southern Iraq.

Description of a new species of *Dermoergasilus planilizai* sp. nov. (Copepoda: Ergasilidae) from abu mullet *Planiliza abu* (Heckel) gills at Al-Gharraf River, Southern Iraq

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Abstract

Dermoergasilus planilizai sp. nov. is described from the gills of the abu mullet *Planiliza abu* (Heckel), the only freshwater member of the Mugilidae occurring in the Mesopotamian region. Specimens were collected from the Al-Gharraf River, southern Iraq. The new species is distinguished from its closest congener, *Dermoergasilus varicoleus* Ho, Jayarajan & Radhakrishnan, 1992, by the following combination of characters: (i) setae on caudal rami distinctly longer than the digitiform process (*vs* shorter); (ii) terminal spines on endopod of leg 1 strongly curved (*vs* straight); and (iii) free segment of leg 5 approximately three times longer than the basal segment (*vs* twice as long).

Key words: Fresh water, Fish, Gills, Copepods, Parasite, Iraq.

Introduction

The Tigris–Euphrates basin forms the principal freshwater drainage of Southwest Asia, situated between the major basins of the Nile to the west, the Indus to the east, and the drainages of the Black and Caspian Seas to the north (Coad, 1996). This region acts as a biogeographic corridor linking Europe, Asia, and Africa, where geological events since the Miocene, including the regression of the Tethys Sea, have created a long-standing land and freshwater bridge that enabled faunal interchange and colonization by primary freshwater fishes. Over the course of the Holocene, repeated hydrological fluctuations have further shaped the basin's ichthyofauna (Oosterbroek & Arntzen, 1992).

Among the characteristic species inhabiting these waters is the abu mullet *Planiliza abu* (Heckel), a freshwater mugilid widely distributed in the Euphrates–Tigris drainage, occurring in marshes and reservoirs across Turkey, Syria, Iraq and Iran (Freyhof *et al*., 2021). Lying at the junction between the Oriental and Palearctic regions, the basin supports a diverse

assemblage of fishes with a high proportion of endemic and relict lineages (Banister, 1980; Coad, 1996). Such environmental heterogeneity and transitional biogeographic position provide exceptional conditions for the diversification of parasitic crustaceans associated with fishes.

The genus *Dermoergasilus* Ho & Do, 1982 currently includes 13 valid species reported from a variety of fishes across Asia, Africa, and Australia. The genus exhibits remarkable variability in host specialization: approximately half of all known species are restricted to a single family, Mugilidae (6 species), while others occur on fishes of Belonidae (2 species), Cichlidae (2 species), and Sparidae (1 species). Only *Dermoergasilus amplectens* (Dogiel & Akhmerov, 1952) has been recorded from as many as 8 host families, whereas *Dermoergasilus occidentalis* Hassan, Jones & Lymbery, 2009 parasitizes 2 different families (Hassan *et al*., 2009; Míč *et al*., 2025; Walter & Boxshall, 2025).

In Iraq, the family Ergasilidae is represented by four genera: *Dermoergasilus*, *Ergasilus* von Nordmann, 1832, *Mugilicola* Tripathi, 1960, and *Paraergasilus* Markevich, 1937 (Mhaisen, 2025). Among these, *Dermoergasilus varicoleus* Ho, Jayarajan & Radhakrishnan, 1992 was first reported from the gills of *Planiliza abu* (syn. *Liza abu*) in the Garmat-Ali River by Khamees & Mhaisen (1995). Subsequently, this copepod was found on 9 host species, including the greenback mullet *Planiliza subviridis* (Valenciennes), 7 cyprinids, and 1 silurid (Ali & Adday, 2019; Mhaisen, 2025). Another Iraqi representative, *Dermoergasilus cichlidus* Ali & Adday, 2019, was described from the gill filaments of the redbelly tilapia *Coptodon zillii* (Gervais, 1848) in Basrah Province (Ali & Adday, 2019). In addition, Ahmed & Ali (2013) recorded *Dermoergasilus* sp. from the gills of *Cyprinus carpio* Linnaeus in ponds of the Marine Sciences Centre, Basrah.

During a recent parasitological examination of *P. abu* from the Al-Gharraf River (a branch of the Tigris drainage in southern Iraq), several specimens of *Dermoergasilus* were collected that differed morphologically from previously described congeners. Their general habitus resembled that of *D. varicoleus*, leading to occasional confusion in earlier records; however, careful study revealed a distinct combination of diagnostic features justifying description as a new species. The present paper provides a detailed description of this copepod, *Dermoergasilus planilizai* sp. nov., parasitic on the gills of *P. abu* in the Al-Gharraf River.

Materials and methods

A total of 102 specimens of the abu mullet *Planiliza abu* ranging from 80 to 215 mm in total length, were collected from the Al-Gharraf River, a southern tributary of the Tigris system in southern Iraq, during October 2024. The gill arches were removed and examined under a stereomicroscope (Optika S2-ST1) for the presence of parasitic copepods.

Collected specimens were carefully detached from the gill filaments using fine needles and preserved in 70% ethanol for subsequent study. For morphological examination, specimens were mounted in 90% lactic acid overnight on glass slides, following the procedure of Adday & Ali (2020), with modification from the traditional wooden-slide method originally proposed by Humes & Gooding (1964).

Morphological observations and drawings were made using a compound microscope (Olympus CX21 FS1) equipped with a drawing tube. All measurements are expressed in micrometres (μm), and the terminology follows the standard descriptive scheme for the family Ergasilidae. Prevalence and mean intensity of infection were calculated according to the definitions of Bush et al. (1997).

The type specimens of the new species, including the holotype and paratypes, are deposited in the Institute of Parasitology, Biology Centre of the Czech Academy of Sciences, České Budějovice (IPCAS, Czech Republic under registration number IPCAS Cr-43.

Results

The copepod specimens collected from *P. abu* were identified as *Dermoergasilus* based on the diagnostic morphological characters according to Ho & Do (1982), specifically: (i) antenna, except terminal claw, covered with inflated transparent membrane; (ii) paired caudal rami each with a digitiform process; and (iii) middle segment of endopod of legs II and III possessing a single seta.

Family Ergasilidae Burmeister, 1835

Genus *Dermoergasilus* Ho & Do, 1982

Dermoergasilus planilizai sp. nov.

Type host: *Planiliza abu* (Heckel) (Mugiliformes: Mugilidae).

Type locality: Al-Gharraf River, Thi Qar Province, southern Iraq.

Site of infection: Gill filaments.

Prevalence: 0.1176%; mean intensity 2–4 (mean 3).

Type material: Holotype female and paratypes (females) deposited in the Institute of Parasitology, Biology Centre of the Czech Academy of Sciences, České Budějovice, Czech Republic under registration number IPCAS Cr-43.

Etymology: The specific name "planilizai" refers to the generic name of the type host *Planiliza*.

Description

Adult female. [Based on 5 specimens; Figs. 1-3; measurements in Table 1].

Body 819–858 μm (mean 839) in total length, slender and elongate (Fig. 1A). Cephalothorax oblong, slightly tapering anteriorly and truncate posteriorly, constituting more than half of total body length (53%), and about 1.54 times longer than wide. A transverse dorsal constriction present at mid-length. The cephalon not distinctly separated from the first pedigerous somite, bearing a narrow anterior and broad posterior margin, with an inverted T-shaped dorsal surface marking.

First pedigerous somite large, about two-thirds the length of the genital somite. Second to fourth pedigerous somites free, broader than long and progressively narrowing posteriorly, each with a distinct dorsal tergum.

Genital double-somite (Fig. 2A) elongate, slightly widest anteriorly, and approximately 1.4 times longer than wide; about 1.5 times longer than the first abdominal somite. A single fine row of spinules present in the posterior third of the genital somite. First free abdominal somite 1.2 × longer than wide and slightly longer than the combined length of the second and third abdominal somites plus caudal rami. Second abdominal somite short, about 0.45 × the combined length of the anal somite and caudal rami. Minute transverse rows of spinules present on the anterior margin of the first abdominal somite and on the posterior margin of the anal somite.

Anal somite shallowly incised medially on posterior border. Caudal rami subrectangular, 1.1 × longer than wide, about 0.9 × length of anal somite, each bearing a digitiform process carrying a short terminal seta. The digitiform process 1.23 × longer than the ramus. The longest caudal seta armed with rows of minute spinules; two lateral setae slightly longer than the digitiform process (Fig. 2B).

Antennule (Fig. 2C) short, 6-segmented, gradually tapering distally. Setal formula: 3, 10, 4, 4, 3, 6 + ae.

Antenna (Fig. 2D) 4-segmented, comprising short coxobasis and 3-segmented endopod terminating incurved claw. Coxobasis elongated, forming well-developed pedestal. The first endopodal segment longest, about 1.7 × as long as coxobasis. The combined length of the

second and third segments with terminal claw equaling 0.98 × the length of the first segment. The terminal claw slightly curved and about half the length of third segment. The entire antenna, except for terminal claw enclosed within an inflated, transparent cuticular membrane characteristic of the genus *Dermoergasilus*.

Mouthparts consisting of mandible, maxillule, and maxilla (Fig. 2B). Mandible unsegmented, bearing three blades; anterior blade armed with teeth on anterior margin, distal and posterior blades bear teeth posteriorly. Maxillule lobate, with two subequal setae. Maxilla 2-segmented; syncoxa robust and tapering distally, basis elongate and spatula-shaped, with marginal rows of small teeth.

Swimming legs (L1–L4) (Figs. 3B–D) biramous, with 3-segmented rami, except for leg 4, which has 2-segmented exopod.

Armature of legs 1-4 as follows (spines: Roman numerals; setae: Arabic numerals):

	Coxa	Basis	Exopod	Endopod
Leg 1	0-0	0-1	I-0; 0-1; II-5	0-1; 0-1; II, 4
Leg 2	0-0	0-1	I-0; 0-1; 0-6	0-1; 0-1; I-4
Leg 3	0-0	0-1	I-0; 0-1; 0-6	0-1; 0-1; I-4
Leg 4	0-0	0-1	I-0; 0-5	0-1; 0-2; I-3

Leg 1 (Fig. 3B). Exopod 3-segmented. First segment bearing a small naked spine on the outer posterior margin; second segment with 1 inner plumose seta; third segment armed with 2 blade-like serrated spines (the proximal shorter), 1 semi-plumose seta (i.e. with serrations along the outer margin) and 4 plumose setae. Endopod 3-segmented; first and second segments each bearing 1 inner plumose seta; third segment armed with three plumose setae, one semi-plumose seta, and two terminal blade-like serrated spines. Inner terminal spine distinctly curved, whereas outer spine straight and longer. Posterior margins of first and second endopodal segments bear minute rows of spinules.

Leg 2 and 3 same in structure (Fig. 3C). Exopod 3-segmented; first segment with small outer spine, second segment with 1 plumose seta; third segment bearing 1 semi-plumose seta and 5 plumose setae. Endopod 3-segmented; first and second segments each carrying 1 plumose seta; third segment bearing 1 small slender serrated spine, 3 plumose setae, and 1 semi-plumose seta

Leg 4 (Fig. 3D). Exopod 2-segmented; first segment elongate, armed with small outer spine; second segment bearing 5 plumose setae. Endopod 3-segmented; first segment with 1 plumose

seta, second segment with 2 plumose setae, and third segment with 1 slender serrated spine and 3 plumose setae.

Interpodal sternites of legs 1–3 broad, each bearing minute rows of spinules along posterior margin.

Leg 5 (Fig. 3E) 2-segmented; proximal segment short, bearing single outer seta. Distal segment elongate, carrying 1 lateral seta and 2 terminal setae. Free (distal) segment about three times as long as basal segment.

Table 1: Comparative metrical data for *D. planilizai* sp. nov. with *D. varicoleus*.

character	*D. varicoleus*	*D. planilizai* sp. nov. Min-max (mean)
Study	Ho et al. 1992; El-Rashidy & Boxshall, 2001	present study,
Total length	648	819–858 (839)
Body width	240	436.8–452.4 (445)
Length Coxabasis of 2nd antenna	-	097.5-109.2 (103)
Length 1st segment length of 2nd antenna	-	169.6-177.4 (174)
Length 2 plus 3 antenna segment length	-	105.3-107.2 (106)
Claw length	-	62.4-68.2 (65)
Ratio segment 2 plus segment 3: segment 1	60	31.3-44.3 (41.6)%
Cephalothorax length	400	436.8–452.4 (445)
Cephalothorax width	240	280.8–312.4 (289)
Thoracic segment 2nd length	65	45.8–50 (65)
Thoracic segment 2nd width	134	117.5–118.1 (118)
Thoracic segment 3rd length	52	45.7–50 (57)
Thoracic segment 3rd width	103	88–87.9 (88)
Thoracic segment 4th length	34	37.9–38 1 (38)
Thoracic segment 4th width	65	29.4–30 (30)
Thoracic segment 5th length	130	15–15.3 (15)
Thoracic segment 5th width	65	64 5–70 0 (66)
Genital double somite length	166	101.1–101.4 (101)
Genital double somite width	113	68.2–72 1 (70)
Abdominal segment 1st length	133	66.3–68.2 (67)
Abdominal segment 1st width	76	54.6–55.9 (56)
Abdominal segment 2nd length	33	17–19 (18)

Abdominal segment 2nd width	63	43–43.5 (43)
Abdominal segment 3rd length	20	21.5–22 (20.9)
Abdominal segment 3rd width	50	39–40 (39.5)
Caudal ramus length	19	17.5–19.5 (19)
Caudal ramus width	12	15.6–17.5 (17.02)
Digitiform process length	----	21.5-23.4 (23.4)
Seta of caudal ramus	----	25.3-33 (28.22)
Egg sac length	753	636–653 (653.22)

Remarks

Dermoergasilus planilizai sp. nov. closely resembles *D. varicoleus* in general body form and in most morphological details. However, it can be readily distinguished from that species by several characters. In *D. planilizai*, the setae on the caudal rami are distinctly longer than the digitiform process, whereas in *D. varicoleus* the caudal setae are shorter than the digitiform process. The terminal spines on the endopod of leg 1 in the new species are strongly curved, while those in *D. varicoleus* are straight. Furthermore, the free (distal) segment of leg 5 is about three times as long as the basal segment, compared with a twofold ratio in *D. varicoleus*.

Quantitative comparison of the antennal proportions also supports the separation of these taxa. In *D. varicoleus*, the combined length of the second and third endopodal segments of the antenna is about 60% of the first segment length, while in *D. planilizai* this ratio is approximately 41.6%. Additional differences occur in the form of the digitiform process and in the relative length of the caudal rami, which are longer and more slender in *D. planilizai* than in *D. varicoleus*.

The presence of strongly curved terminal spines on the endopodal segment of leg 1 further relates the new species to *Dermoergasilus coleus* (Cressey in Cressey & Collette, 1970), *Dermoergasilus intermedius* (Kabata, 1992), and *Dermoergasilus mugilis* Oldewage & Van As, 1988, all of which possess a similar modification of the terminal spines. However, *Dermoergasilus planilizai* sp. nov. differs from these species in the setal formula of legs 1–4 and in the structure of the antenna. Specifically, *D. coleus* and *D. mugilis* exhibit differing armature patterns on both rami of legs 1–4, whereas *D. intermedius* differs in the number of setae on the endopods of legs 2–4.

Discussion

According to the definition provided by Ho & Do (1982), members of the genus *Dermoergasilus* are characterized by three principal diagnostic features: (i) the antenna, except for its terminal claw, is enclosed within an inflated transparent membrane; (ii) each caudal ramus bears a distinct digitiform process; and (iii) the middle segment of the endopods of legs 2 and 3 each carries a single seta. The present specimens possess all these defining traits and can therefore be confidently assigned to the genus *Dermoergasilus*.

Within the genus, *Dermoergasilus planilizai* sp. nov. shows overall morphological similarity to a number of species within the genus, particularly those sharing a relatively slender body form, moderately inflated antennal membrane, and a comparable armature of swimming legs. Such morphological conservatism seems to be a defining feature of *Dermoergasilus* and often complicates the recognition of species boundaries. Nevertheless, the consistent proportional differences of the antenna, the elongation of the caudal rami, and the characteristic curvature of the terminal spines on leg 1 distinguish it as an independent taxon.

The new species appears morphologically allied to *Dermoergasilus curtus* El-Rashidy & Boxshall, 2001, *D. intermedius* and *Dermoergasilus madagascarensis* Míč, Řehulková, Šimková, Razanabolana & Seifertová, 2024, which also possess only slightly inflated antennal membranes. These species together may represent a structural subgroup within the genus characterized by a reduction in antennal expansion and a preference for hosts inhabiting freshwater or marginally brackish environments. The moderate degree of modification in *Dermoergasilus planilizai* sp. nov. may suggest adaptation to the gill microhabitat of its freshwater mugilid host, *Planiliza abu*, the only representative of the family Mugilidae inhabiting the inland waters of Mesopotamia.

The present record from the Al-Gharraf River extends the known range of *Dermoergasilus*. This genus is widespread across tropical and subtropical waters, with most described species originating from the Oriental region, where its diversity appears to be greatest. The concentration of species in South and Southeast Asia, together with additional representatives in Africa and Madagascar, indicates that the genus may have an Oriental evolutionary origin, followed by dispersal and diversification associated with their respective hosts occupying coastal and freshwater systems.

Within Iraq, the family Ergasilidae is represented by several genera (*Dermoergasilus*, *Ergasilus*, *Mugilicola* and *Paraergasilus*) reflecting a relatively high diversity of gill-parasitic copepods in the region. The discovery of *Dermoergasilus planilizai* sp. nov. adds a further element to this fauna and demonstrates that Iraqi inland waters, particularly the Tigris–Euphrates drainage, support a distinct ergasilid assemblage. Continued parasitological

exploration of the Mesopotamian ichthyofauna is therefore likely to reveal additional undescribed species and may contribute valuable evidence to the reconstruction of the biogeographic history of ergasilid copepods in this region and within the whole family.

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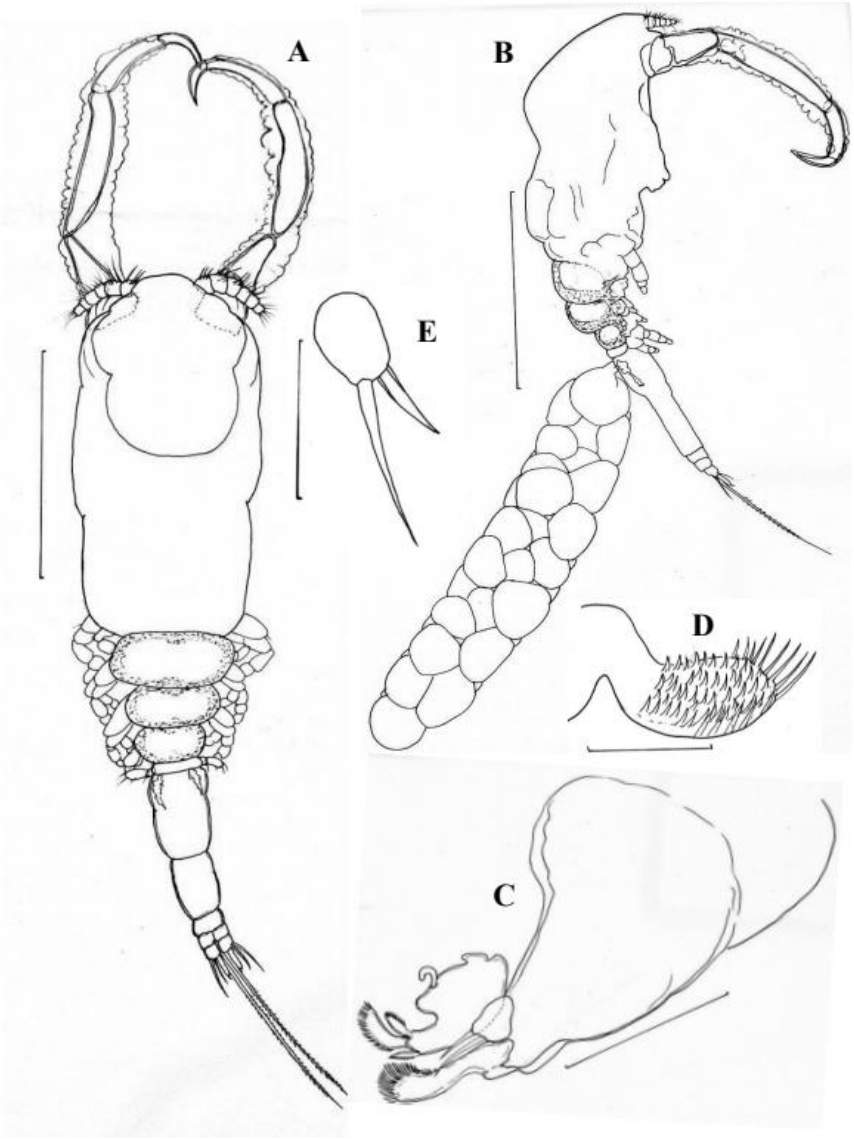


Fig. (1): *Dermoergasilus* sp., adult Female *Planiliza abu*, A habitus, dorsal; B habitus, ventral; C mouth parts; D tip of maxilla; E maxillule (Scale bars 250 µ in A; 50 µ in B, C, D & E).

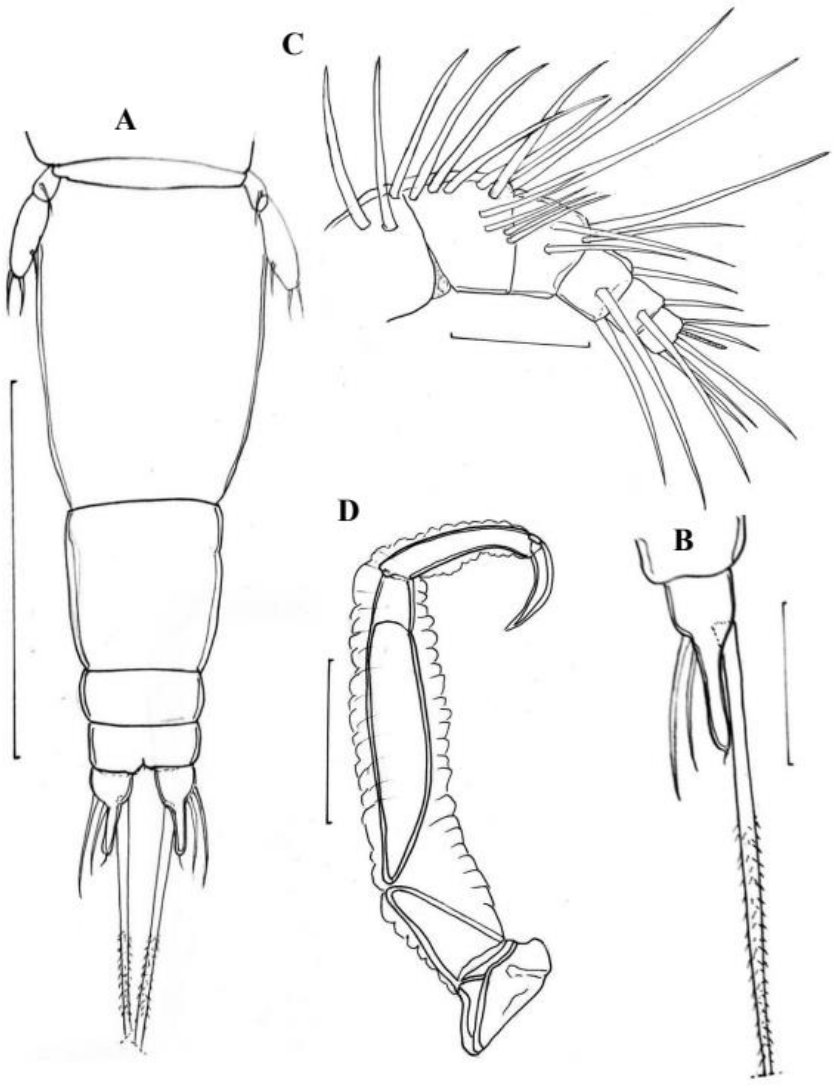


Fig. (2): *Dermoergasilus* sp., adult Female *Planiliza abu*, A urosome; B caudal ramus; C antennule; D antenna (Scale bars 100 µ in A; 50 µ in B, C& D).

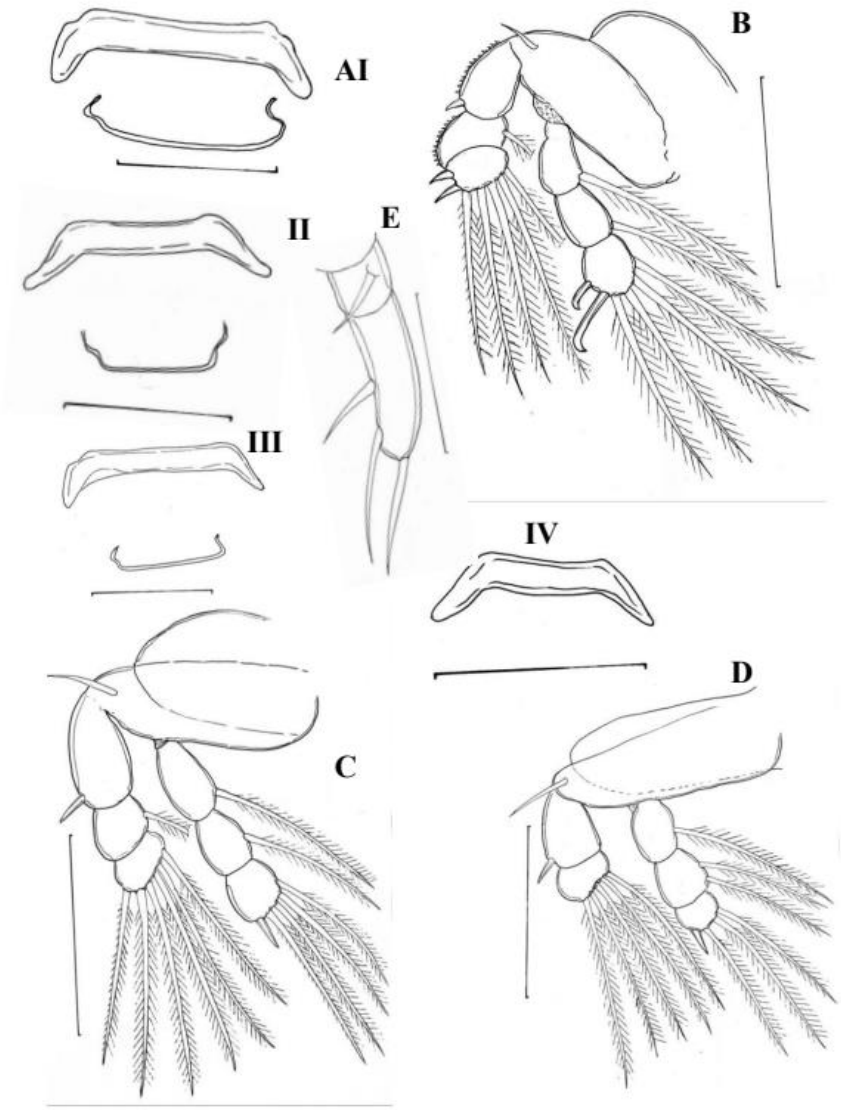


Fig. (3): *Dermoergasilus* sp., adult Female *Planiliza abu*, interpodal plates leg 1to leg 4; B leg 1; C leg 2; D leg 4; E leg 5(Scale bars 50 µ in A; 100 µ in B, in B, C & D).

Paper 6

Kvach, Y., Tkachenko, M. Y., Giannetto, D., **Míč, R.**, Bartáková, V., Ağdamar, S., Saç, G., Özuluğ, M., Tarkan, A. S., & Ondračková, M. (2024). Low Genetic and Parasite Diversity of Invasive Pumpkinseed Lepomis gibbosus (Centrarchidae) Expanding in Türkiye. Diversity, 16(5), 272. https://doi.org/10.3390/d16050272

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Low Genetic and Parasite Diversity of Invasive Pumpkinseed *Lepomis gibbosus* (Centrarchidae) Expanding in Türkiye

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Abstract: Multiple factors can facilitate invasion success, with the absence of natural enemies, such as predators and parasites, recognised as conferring a significant advantage on invasive over native species. Pumpkinseed *Lepomis gibbosus* (Centrarchidae) represents one of the most successful freshwater fish invaders in Europe. Previous research has highlighted genetic differences between pumpkinseed populations in Türkiye and those in other European regions, attributed to rapid adaptation to new environmental conditions. This study aimed to investigate whether these highly adapted pumpkinseed populations in Türkiye benefit from a potential release from parasites, as proposed by the enemy-release hypothesis. Genetic characterisation of pumpkinseed populations from both European and Asian parts of Türkiye revealed that they share the same cytochrome *c* oxidase I haplotype as European populations. Microsatellite analysis indicated low genetic diversity, with STRUCTURE analysis confirming the clustering of all Turkish populations, suggesting a common source. Consistent with the low genetic diversity indicative of a small founding population, we observed a limited number of co-introduced parasite species, including the myxozoan *Myxobolus dechtiari*, the monogenean *Onchocleidus dispar*, and the digenean *Posthodiplostomum centrarchi*. Parasite infection by local parasites acquired in Türkiye was rare. Parasite diversity, species richness, and equitability were low, with only nine parasite taxa identified in all four pumpkinseed populations. The most diverse parasite community was found in Değirmenköy Reservoir, located in the European part of Türkiye, where seven parasite taxa were identified. While our study did not uncover genetically distinct pumpkinseed populations in Türkiye, the fish demonstrated resilience against most local parasite species, potentially providing them with an advantage over native species, aligning with the enemy-release hypothesis.

Keywords: microsatellites; cytochrome *c* oxidase I; parasitism; species introductions; Türkiye

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1. Introduction

Fish play a crucial role in the economies of many countries, yet risk management measures, such as quarantine controls, are often less stringent than for other animals [1].

The incidence of freshwater fish introductions has surged in recent decades due to the expansion of global trade, and this trend is expected to persist in the coming years [2,3]. The unintentional release or escape of introduced fish into natural habitats, resulting in invasive populations that disrupt native ecosystems, serves as a prime example of the socio-economic, ecological, and evolutionary impacts of globalisation on local biodiversity [4–7]. The adverse effects of non-native species on indigenous fauna encompass predation, competition for food and space, hybridisation, alteration of food webs and biogeochemical cycles, as well as the transmission of parasites and pathogens [4,8]. In particular, non-native fish parasites are a global problem affecting aquaculture and natural ecosystems worldwide [9,10].

Pumpkinseed (*Lepomis gibbosus* (L., 1758), Actinopterygii: Centrarchidae) is a species indigenous to freshwater habitats in eastern North America, ranging from New Brunswick, Canada, to north-eastern Georgia, USA [11]. Initially introduced to Europe as an ornamental fish in 1877, transported from Canada to Paris [12], the species was subsequently released into open waters, primarily in southwestern France, where stable populations were established around 1900 [13,14]. Over the following century, the pumpkinseed was introduced to nearly all European countries and has recently become an invasive species across much of the continent, spanning from the Iberian Peninsula in the west to coastal rivers of the Sea of Azov in the east [15,16]. In Türkiye, the fish was first documented in the Ipsala Canal (Meriç River drainage) in 1982 [17]. In the Asian part of Türkiye, it was initially observed in the Sarıçay and Dipsiz-Çine streams (Muğla, Anatolia) between 1999 and 2001 [18–20], subsequently spreading throughout the Aegean Region of Anatolia [21–26]. More recently, the fish has expanded into numerous new habitats in the Marmara and Aegean regions, encompassing both the European and Asian parts of Türkiye [27,28]. Currently, Anatolia represents the sole Asian region where the invasive pumpkinseed is established. However, other Asian countries, such as China, Iran, Japan, and South Korea, have experienced introductions of another invasive centrarchid fish, the bluegill (*Lepomis macrochirus* Rafinesque, 1819), in the past [29–32].

Molecular genetic studies of invasive species offer valuable insights into their characteristics, evolutionary processes, and genetic adaptations that contribute to their successful establishment in new environments [33]. Such analyses also aid in elucidating the origin and invasion history of these species [34]. European populations of pumpkinseed have been extensively investigated using both mitochondrial [21,35–37] and nuclear [38] gene markers, revealing generally low genetic variability. In contrast to other European populations, where all pumpkinseed populations are associated with a single haplotype of cytochrome *c* oxidase I (*cox1*) mitochondrial DNA [35,36], higher *cox1* diversity has been observed in Türkiye [21,39]. The three *cox1* haplotypes identified in Türkiye differ from, yet are derived from, the common haplotype found in other European and North American pumpkinseed populations, suggesting the species' evolutionary adaptability under the influence of different selection pressures, such as environmental factors [21].

In addition to abiotic environmental factors like temperature or salinity, non-native species face pressure from biotic factors such as parasitism. The role of parasites in the success of invasive species has gained widespread recognition, with parasites significantly influencing interactions between non-native and native species [40]. Non-native species may introduce new parasite species into the invaded ecosystems, which could be specific to their original hosts, as well as the agents of diseases for the local fauna [41]. Release from pressure by natural parasites advantaging non-native species over natives is among the most commonly proposed hypotheses regarding the role of parasites in biological invasions [42]. There has been an increased interest in the investigation of pumpkinseed parasites in various non-native European populations in Europe during the recent decades, revealing considerable variation in parasite abundance and diversity across different geographical regions, time since introduction, and host genetic diversity [36,38,43,44]. Studies on parasite communities have identified a range of North American parasite species co-introduced to Europe with pumpkinseed, including myxozoans [45], centrarchid-specific

monogeneans [38,46–48], cestodes [49], and trematodes [50,51]. However, these studies have predominantly focused on pumpkinseed populations of the common *cox1* haplotype.

Therefore, the main objective of this study was to investigate parasite communities of pumpkinseed in Türkiye, where different haplotypes and high environmental tolerances of this fish species have recently been observed [21]. We expected that genetically reduced pumpkinseed populations derived from the common haplotype found in other European populations indicating the rapid evolutionary adaptability to new environmental conditions [21] would exhibit low parasite diversity and abundance, especially regarding co-introduced parasite species [38,52]. Reduced genetic diversity related to small founder populations may be associated with a decreased probability of parasite transmission to new areas due to their absence in the founding population or presence at such low densities that the parasite population cannot be sustained [52]. To confirm the genetic variability of fish collected in Türkiye, we conducted a molecular analysis using both mitochondrial (*cox1*) and nuclear (microsatellites) markers, comparing the obtained results with those of fish collected in various European localities as published by Ondračková et al. [36,38]. This study also presents the first data on parasite communities in pumpkinseed that were introduced to Asia.

2. Materials and Methods

2.1. Fish Sampling

The fish were sampled from four locations in Türkiye in October 2021 (Figure 1). Two of these locations were situated in the Aegean region of Anatolia. These locations were Sarıçay River (37.316111, 27.706667) and Dipsiz-Çine Stream (37.763889, 27.833611). One location was in north-western Anatolia—Davuldere Reservoir (40.907186, 30.039250), and one was in the European part of the City of Istanbul—Değirmenköy Reservoir (41.166692, 28.017958). According to Ağdamar et al. [21], fish from Davuldere Reservoir corresponded to *cox1* haplotype H_2 and those from Sarıçay River to H_3, while fish from Dipsiz-Çine Stream and Değirmenköy Reservoir had not been genotyped previously.

Electrofishing using backpack electrofishing gear (SAMUS 725G and SAMUS 1000) was the preferred method for fish sampling for parasitological investigation [53]. The fish were transported alive in aerated river water to the laboratory, where they were placed into aerated tanks with water from the sampling sites. All fish were dissected within three days of sampling to ensure maximum parasite recovery (see [54]). Before dissection, the standard length (SL, mm), total length (TL, mm), total weight (W, g), and eviscerated weight (Wb, g) were measured for each fish (Table 1), and a sample of the caudal fin was preserved in 96% ethanol for further molecular analysis.

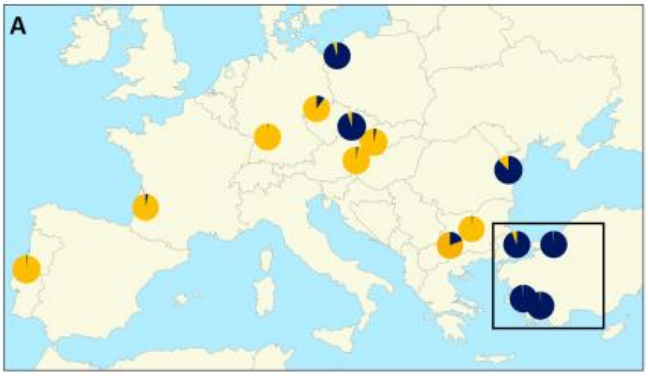


Figure 1. *Cont.*

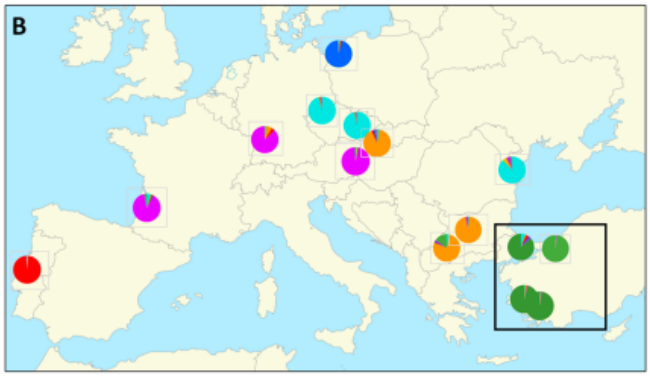


Figure 1. Map indicating the populations of pumpkinseed *Lepomis gibbosus* compared in this study. Populations from Türkiye are marked by black frames. Based on the STRUCTURE analysis, dividing into two (**A**) and six (**B**) clusters (marked by different colours) was identified as the best-supported model of population structuring.

Table 1. Size and weight of the sampled fish in Türkiye. SL—standard length, TL—total length (in mm), W—total weight, We—eviscerated weight (in g).

Locality		SL, mm	TL, mm	W, g	We, g
Sarıçay River (n = 21)	M ± sd	70.4 ± 4.8	86.2 ± 5.9	11.4 ± 2.6	11.0 ± 2.6
	Min–max	61.4–77.4	77.3–97.8	7.5–16.7	7.3–16.3
Dipsiz-Çine Stream (n = 20)	M ± sd	48.3 ± 21.8	59.0 ± 26.3	5.9 ± 11.5	5.7 ± 11.2
	Min–max	28.6–110.3	35.8–133.9	0.7–41.1	0.6–39.9
Davuldere Reservoir (n = 20)	M ± sd	48.1 ± 6.8	59.4 ± 8.1	2.9 ± 2.0	2.8 ± 2.0
	Min–max	42.7–74.3	52.1–90.4	1.8–11.3	1.6–11.2
Değirmenköy Reservoir (n = 20)	M ± sd	57.4 ± 19.4	70.4 ± 24.2	7.6 ± 9.4	7.3 ± 8.9
	Min–max	40.6–98.4	50.1–119.7	1.6–29.2	1.6–28.0

2.2. Genetic Analysis of Fish

The DNA of the fish was extracted using the commercial GeneJETTM Genomic DNA Purification Kit (Thermo Scientific, Waltham, MA USA) following the enclosed instructions. For 31 fish, the partial mitochondrial *cox1* gene was amplified using the primers Fish-F1 (5′TCAACCAACCACAAAGACATTGGCAC3′) and Fish-R1 (5′TAGACTTCTGGGTGGCC AAAGAATCA3′) [55] with the PCR Multiplex Kit (Qiagen, Hilden, Germany) under standard protocol and an annealing temperature of 58 °C. The PCR products were commercially sequenced at Eurofins Genomics Germany GmbH and analysed using Geneious v.9.0.5. software (http://www.geneious.com). Samples from 81 fish individuals from the four localities were genotyped for five polymorphic microsatellite loci (Lmar9, Lmar18, Lmar29, RB7, and RB20) with the PCR details described by Ondračková et al. [38]. The PCR products were electrophoresed on the ABI Prism®3130 Genetic Analyser (Applied Biosystems, Foster City, CA, USA) and analysed using Geneious.

Genetic divergence among populations was estimated by pairwise FST [56] using 1000 permutations in GENETIX 4.05 [57]. The Hardy–Weinberg equilibrium (HWE) test was performed for each locus in all populations using the Markov chain method ("Exact probability test") in Genepop v.4.7 [58]. The number of different alleles (NA), the Shannon information index (I), expected heterozygosity (He), unbiased expected heterozygosity (UHe), observed heterozygosity (Ho), fixation index (F), and percentage of polymorphic loci (P) were all calculated in GenAlEx v. 6.51 [59,60]. Newly generated sequences of one specimen per locality were deposited in the GenBank database under accession numbers PP469740-PP469743.

The population genetic structure was analysed using the Bayesian clustering algorithm implemented in the program STRUCTURE v. 2.3.4 [61]. The program was run with 10 independent simulations for each K from 1 to 10, with 1 million iterations for each simulation (burn-in = 100,000 iterations) using an admixture model and a correlated allele frequencies model (λ = 1). The output of the STRUCTURE analysis was post-processed using CLUMPAK software v. 1.1 [62] to identify separate groups of runs based on similarity between Q-matrices for each K using the LargeKGreedy algorithm, random input order, and 2000 repeats. Different modes were identified for similarity scores from the 20 runs for each K value at a threshold of 0.9. The web-based software STRUCTURE HARVESTER v. 0.7 July 2022 [63] was used to summarise output data from STRUCTURE. The likelihood of K (Ln Pr(X | K)), the ΔK criterion using the method of Evanno et al. [64], and a proportion of similar runs that formed the major modes for each K were used to infer the best number of real populations in the datasets.

2.3. Parasite Collection, Processing and Analysis

A total of 81 individual fish were examined for parasites (Table 1). The fins, skin, gills, muscles, and internal organs were inspected for parasites. Myxozoans were examined live using light microscopy and photographed for further identification. Monogeneans were preserved in GAP (glycerine-ammonium-picrate) and prepared as semi-permanent slides [65] while digeneans and nematodes were preserved in hot 4% formaldehyde, with digeneans stained with iron acetic carmine, dehydrated in ethanol of increasing concentration, and mounted in Canada balsam as permanent slides [66,67]. Crustaceans were preserved in 4% formaldehyde and identified under light microscopy. All parasites were identified based on their morphological features at the species level where possible or at the highest taxonomic level when species-level identification was impossible. A subsample of larval digeneans and nematodes, where morphological identification is difficult, was preserved in 96% ethanol for further molecular analysis.

The DNA of parasites (larval digeneans and nematodes) was extracted using the Invisorb® Spin Forensic Kit (STRATEC Molecular, Berlin, Germany) following the standard protocol. We used forward primer BD1 (5′-GTCGTAACAAGGTTTCCGTA-3′) and the reverse primer 4S (5′-TCTAGATGCGTTCGAA(G/A)TGTCGATG-3′) [68] to obtain the ITS1 partial sequence for *Posthodiplostomum*, with an annealing temperature of 58 °C (PCR details in [43]). For obtaining the 18S partial sequence for nematodes, we employed the forward primer 18S-CL-F3 (5′-CTTGTCTCAAAGATTAAGCCATGCAT-3′) [69] and the reverse primer D2AR (5′-ACTTTCCCTCACGGTACTTGT-3′) (reverse of D2A from [70]). The reaction mix contained 4 µL of extracted DNA, 0.3 µL of each primer (10 µM), 2 µL of buffer A, 0.2 µL of dNTPs (10 mM), 0.2 µL of MgCl2 (25 mM), 0.5 U/µL of Taq polymerase, and ddH2O up to a total volume of 10 µL. For PCR analysis, we used the KAPA2G Robust HotStart PCR Kit (Kapabiosystems, Wilmington, MA, USA), with amplification conducted in a Mastercycler ep gradient S thermocycler (Eppendorf, Hamburg, Germany) following a temperature profile of the PCR reaction of 95 °C for 2 min, 5 cycles of (94 °C for 30 s, 45 °C for 40 s, 72 °C for 2 min), 40 cycles of (94 °C for 30 s, 58 °C for 40 s, 72 °C for 2 min), and a final extension at 72 °C for 5 min. All PCR products were purified using an ExoSAP-IT kit (Affymetrix Inc., Santa Clara, CA, USA) per the manufacturer's protocol. Subsequently, the PCR products were commercially sequenced at Eurofins Genomics Germany GmbH. The sequences were checked and aligned using Geneious, and the newly generated sequences were compared with the NCBI database using BLASTn to assess sequence similarity.

Prevalence, intensity of infection, and abundance were calculated following Bush et al. [71]. Mean abundance was expressed as the mean number of parasites for all hosts in a sample, intensity of infection as the mean number of parasites for infected hosts, and prevalence as the percentage of infected hosts. The parasite community was analysed at both the infracommunity (IC, including all parasites on a single host) and component community (CC; all parasites in a host population) levels [71]. Similarity in parasite communities was evaluated based on qualitative and quantitative data on parasite species

composition using the Sørensen and Bray–Curtis similarity indices, respectively. Diversity, describing the relationship of the ratios of all parasites in a host population or specimen, was calculated by the Shannon–Wiener index (H). Equitability (J) was used to measure the evenness with which individuals are distributed among the taxa present [72]. The trend for parasites to appear in the same IC was expressed by the infracommunity index (ICI). The ICI describes the frequency of double and multiple infections by a single parasite species in a distinct host [73]. Values > 0.4 indicate strongly interactive parasite species, >0.3 indicate a great tendency to join the community, while values > 0.2 suggest moderately interactive parasite species [73,74].

3. Results

3.1. Genetic Characterisation of Fish Host

All four pumpkinseed populations sampled in Türkiye exhibited a single *cox1* haplotype. The partial *cox1* sequences ranged between 630 and 636 bp in length and corresponded to those obtained from fish collected in other non-native European (GeneBank accession numbers KY231843, MW473462, HQ600737, KJ553720, MK439905) as well as native North American (KX145030, MF621725, KX145396, KX145175, KX145351, MF621724, MT667250, MF621726, JN026988) populations. A total of 19 alleles were observed for the five microsatellite loci, with four loci being polymorphic, while Lmar9 had a single allele in all four populations. All four populations were in Hardy–Weinberg equilibrium, and values of total and average allele richness, number of effective alleles, Shannon information index, and heterozygosity, as shown in Table 2, were similar among particular populations. Three private alleles were observed at each of the Davuldere and Değirmenköy Reservoirs.

Table 2. Results of testing of genetic variability for five microsatellite loci. N = No. of individuals; NA = number of different alleles, I = Shannon's Information Index; Ho = Observed Heterozygosity; He = Expected Heterozygosity; uHe = Unbiased Expected Heterozygosity; F = Fixation Index; HWE = P-values of Hardy–Weinberg Equilibrium; P = Percentage of Polymorphic Loci.

Population	N	NA	I	Ho	He	Uhe	F	HWE	%P
Sarıçay River	21	2.400	0.579	0.333	0.362	0.370	0.074	0.940	80
Dipsiz-Çine Stream	20	2.000	0.434	0.280	0.281	0.288	−0.021	0.993	80
Davuldere Reservoir	20	2.600	0.572	0.330	0.310	0.318	−0.066	0.429	60
Değirmenköy Reservoir	20	2.400	0.658	0.450	0.427	0.438	−0.080	0.520	80

STRUCTURE analysis conducted using fish from four populations in Türkiye and 11 other European localities [38] suggested that K = 2 and 6 are the most supported models of population structuring, based on a combination of the likelihood of K (Ln Pr(X | K)), the ΔK criterion [64], and the proportion of similar runs. For K = 2, the two clusters corresponded to (1) Türkiye (all four localities) + Kartal (Ukraine) + Jez (Czech Republic) + Gryfino Canal (Poland) and (2) localities in the basins of the rivers Danube (Austria, Bulgaria, Slovakia), Rhine (Germany), Elbe (Czech Republic), Girone (France), and Sado (Portugal) (Figure 1A). For K = 6, all populations from Türkiye formed a separate cluster, while Değirmenköy Reservoir was partially mixed with other European populations (Figure 1B).

3.2. Composition of Parasite Communities

Nine parasite taxa were found to infect pumpkinseed at four sites in western Türkiye, including one myxozoan, one monogenean, one digenean, five nematodes, and one crustacean (Table 3). Six parasite taxa were in larval stages, including the metacercariae of a digenean and all nematodes, which were all endoparasites located in internal organs, mesentery, and muscles. Ectoparasites were represented by myxozoans and monogeneans infecting gills and a parasitic copepod found on the fins or penetrating the body cavity. Three species, namely myxozoan *Myxobolus dechtiari* Cone and Anderson, 1977, monoge-

nean *Onchocleidus dispar* (Mueller, 1936), and metacercariae of *Posthodiplostomum centrarchi* Hoffman, 1958, were introduced to Europe and are natural parasites of pumpkinseed in North America. These species had relatively high abundances and prevalence (Table 3). Identification of *P. centrarchi* was confirmed through both morphology and genetic analysis, with two sequences obtained from the Sarıçay River (Asia) and one from Değirmenköy Reservoir (Europe). One of the sequences from the Sarıçay River and the Değirmenköy Reservoir were identical and differed from the second sequence from the Sarıçay River with one substitution. All sequences showed 99.9–100% correspondence with *P. centrarchi* from pumpkinseed collected in the Hudson River in Canada (GeneBank Acc. No. MH521251), Hungary (MN080282), and in Portugal (MF171006; denoted as *P. cf. minimum*).

Table 3. Prevalence, mean abundance, species richness, mean infracommunity (IC) richness, Shannon and Equitability indices of parasite communities of the invasive pumpkinseed in four localities in Türkiye. **Bold**: greater part of homogeneity.

Locality	N	Prevalence (in %)	Mean Abundance	Species Richness	Mean IC (MI ± sd)	Shannon	Equitability
Sarıçay River	21	100	124.5	3	2.05 ± 0.65	0.25	0.23
Dipsiz-Çine Stream	20	25	0.5	5	0.30 ± 0.56	1.47	**0.91**
Davuldere Reservoir	20	70	2.5	2	0.75 ± 0.54	0.10	0.14
Değirmenköy Reservoir	20	90	8.8	7	1.70 ± 1.10	1.24	0.64

Out of all parasite taxa pumpkinseed acquired in Türkiye, only two nematodes were found in higher prevalence in Sarıçay River, namely larvae of *Eustrongylides* sp. (57% of fish infected) and larvae of *Parquimperia tenerrima* (von Linstow, 1878) Baylis, 1934 (48% of fish infected), with higher abundance (6.6) observed in the latter. Other taxa acquired in Türkiye (i.e., Aquariidae gen. sp., *Contracaecum* sp., Nematoda sp., *Lernaea cyprinacea* (Linnaeus, 1758)) occurred rarely. Larvae of *Eustrongylides* sp. Were found in all four localities. Both nematode species were subjected to genetic analysis. A sequence of 18S rDNA 775 bp long obtained from *P. tenerrima* (Sarıçay River) showed the highest similarity to *P. africana* (99.6%; difference by three substitutions) from *Anguilla marmorata* Quoy & Gaimard, 1824 in South Africa (JF803925). Larvae of *Eustrongylides* (18S rDNA, 849 bp) obtained from the Dipsiz-Çine Stream and Sarıçay River showed the highest similarity (with query cover > 80%) to *Eustrongylides* sp. (99.6 and 99.4%; difference caused by 1 substitution and one gap, and four unreadable bases, respectively) from *Alligator sinensis* Fauvel, 1879 in China (PP236907).

Maximum parasite prevalence (100%) was found in the Sarıçay River (Table 4). The IC species richness ranged from 0 to 4 per fish. All types of infracommunities were observed only in Değirmenköy Reservoir. Three species IC were found in the Sarıçay River, while two species IC were observed in the Dipsiz-Çine Stream and Davuldere Reservoir (Figure 2). Two parasite species occurred as strongly interactive in the parasite community, i.e., *O. dispar* in the Davuldere Reservoir and *P. centrarchi* in the Sarıçay River. Both species had a clear tendency to join the community in Değirmenköy Reservoir, together with larval nematodes Aquariidae gen. sp. In the Dipsiz-Çine Stream, all parasite taxa were moderately interactive (Table 5).

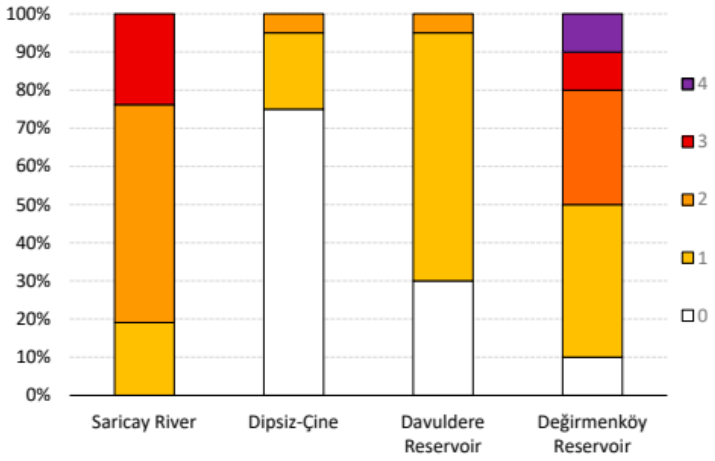


Figure 2. The representation of infracommunities (ranging from zero to four parasite taxa per fish individual) of the invasive pumpkinseed in different localities in Türkiye.

Table 4. Infection parameters of pumpkinseed *Lepomis gibbosus* from four localities in Türkiye: P—prevalence, in %; MI—mean intensity ± standard deviation and minimum—maximum range; and A- mean abundance.

Parasite Species	Site	Indices	Sarıçay River	Dipsiz-Çine Stream	Davuldere Reservoir	Değirmenköy Reservoir
MYXOZOA						
Myxobolus dechtiari	Gills	P, % MI ± sd (min–max) A				15.0 15.3 ± 8.1 (6–20) 2.30
MONOGENEA						
Onchocleidus dispar	Gills	P, % MI ± sd (min–max) A			70.0 3.4 ± 2.3 (1–8) 2.40	55.0 1.6 ± 0.8 (1–3) 0.90
DIGENEA						
Posthodiplostomum centrarchi	Mesentery, liver, spleen, heart, gonads, muscles, head, eyes, coelom	P, % MI ± sd (min–max) A	100.0 117.5 ± 48.0 (48–223) 117.5	5.0 3.0 (3) 0.15		60.0 7.7 ± 11.4 (1–41) 4.60
NEMATODA						
Eustrongylides sp.	Mesentery	P, % MI ± sd (min–max) A	57.1 1.6 ± 0.7 (1–3) 0.9	5.0 1.0 (1) 0.05	5.0 1.0 (1) 0.05	5.0 1.0 (1) 0.05
Contracaecum sp.	Mesentery	P, % MI ± sd (min–max) A		10.0 2.0 ± 1.4 (1–3) 0.2		10.0 1.0 (1) 0.1
Paraquimperia tenerrima	Mesentery	P, % MI ± sd (min–max) A	47.6 13.9 ± 21.8 (1–70) 6.6			

Table 4. *Cont.*

Parasite Species	Site	Indices	Sarıçay River	Dipsiz-Çine Stream	Davuldere Reservoir	Değirmenköy Reservoir
Aquariidae gen. sp.	Intestine wall, mesentery	P, %				20.0
		MI ± sd (min–max)				3.8 ± 2.4 (1–7)
		A				0.75
Nematoda gen. sp.	Liver	P, %		5.0		
		MI ± sd (min–max)		1.0 (1)		
		A		0.05		
COPEPODA *Lernaea cyprinacea*	Fins, mesentery	P, %		5.0		5.0
		MI ± sd (min–max)		1.0 (1)		1.0 (1)
		A		0.05		0.05

Table 5. Infracommunity index of parasite species infecting the invasive pumpkinseed in four localities in Türkiye. **Bold**: parasite species with great tendency to join the infracommunity.

Parasite Species	Sarıçay River	Dipsiz-Çine Stream	Davuldere Reservoir	Değirmenköy Reservoir
Myxobolus dechtiari				0.09
Onchocleidus dispar			**0.93**	0.32
Posthodiplostomum centrarchi	**0.49**	0.17		0.35
Eustrongylides sp.	0.28	0.17	0.07	0.03
Contracaecum sp.		0.33		0.09
Paraquimperia tenerrima	0.23			
Aquariidae gen. sp.				0.31
Nematoda gen. sp.		0.17		
Lernaea cyprinacea		0.17		0.03

3.3. Parasite Diversity

The parasite species richness ranged from two (Davuldere Reservoir) to seven taxa (Değirmenköy Reservoir) (Table 3). High Shannon–Weiner diversity (H = 1.47) and equitability of the parasite community (J = 0.91) were found in the Dipsiz-Çine Stream; nevertheless, most of the fish (75%) at this locality were uninfected, and infected fish were parasitised with low intensities. Low diversity was observed in the Davuldere Reservoir and Sarıçay River (H < 0.25), with these 2 locations demonstrating the lowest equitability values (J = 0.14 and 0.23, respectively).

3.4. Similarity in Parasite Communities

Qualitative and quantitative similarities between parasite communities of pumpkinseed from particular localities are presented in Table 6. The highest qualitative similarity in parasite communities measured by the Sørensen index was observed between Dipsiz-Çine Stream and 2 other localities, Değirmenköy Reservoir (67%) and Sarıçay River (50%). Quantitative similarity measured by the Bray–Curtis index was generally very low, with the highest values found between Davuldere Reservoir and Değirmenköy Reservoir (17%) and the minimum similarity found between Davuldere Reservoir and Dipsiz-Çine Stream (29% for Sørensen) and Davuldere Reservoir and Sarıçay River (0.1% for Bray–Curtis; Table 6, Figure 3).

Table 6. Matrix of qualitative (Sørensen index, below diagonal) and quantitative Bray–Curtis index (above diagonal) similarities between parasite communities of pumpkinseed *Lepomis gibbous* sampled in four localities in Türkiye.

	Sarıçay River	Dipsiz-Çine Stream	Davuldere Reservoir	Değirmenköy Reservoir
Sarıçay River		0.003	0.001	0.067
Dipsiz-Çine	0.500		0.034	0.076
Davuldere Reservoir	0.400	0.286		0.170
Değirmenköy Reservoir	0.400	0.667	0.444	

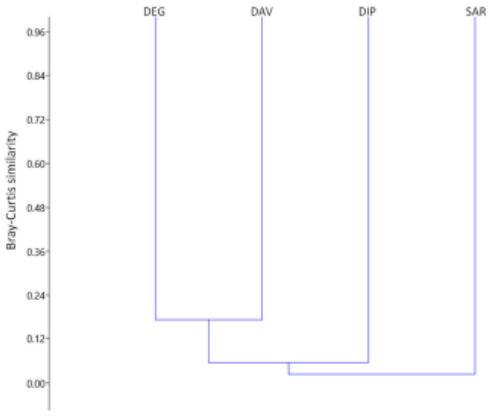


Figure 3. Dendrogram on Bray–Curtis similarity between parasite communities of *Lepomis gibbosus* at four localities in Turkey. DEG—Değirmenköy Reservoir, DAV—Davuldere Reservoir, DIP—Dipsiz-Çine Stream, SAR—Sarıçay River.

4. Discussion

Pumpkinseed collected at four localities in Türkiye exhibited low genetic variance in both mitochondrial and nuclear markers. All fish analysed were associated with a single *cox1* haplotype. The same haplotype was previously found in other non-native populations in Europe [21,35,36] and many native populations in North America [21]. Despite previous studies revealing two different haplotypes at Sarıçay River and Davuldere Reservoir [21,39], our study failed to find these at the same localities ten years later. Pumpkinseed dispersal through Türkiye since its first record in the Turkish Thrace Region [17] followed the pathways of carp stocking, with extensive fish production facilities in the western part of Türkiye being the most probable source [21], and subsequent spread facilitated by local fishermen [75]. However, the reason for our failure to collect fish with the previously detected haplotypes remains a question. One possible explanation might be associated with multiple introductions to the same water bodies with ongoing stockings in Türkiye. According to Ağdamar et al. [21], common carp-rearing ponds in Türkiye are often affected by seasonal floods from the Meriç River, which can lead to the invasion of non-native fish in nearby large fish production units. Similar unintentional introduction through transboundary river systems was reported for *Heteropneustes fossilis* (Bloch, 1794) in the Dicle–Fırat (Tigris–Euphrates) River system [76,77]. As pumpkinseed in Greece belongs to the common European *cox1* haplotype [35], it is possible that subsequent carp stockings unintentionally co-introduced pumpkinseed of this haplotype over ten years, leading to its dominance at the localities. Additionally, there may be natural changes in the occurrence and detection of haplotypes over time due to sampling efforts or stochastic processes [78].

Although new haplotypes were detected in 2015, they may have been present but not detected in 2021 owing to the smaller sampling size.

Results obtained from microsatellite data further supported the common origin of pumpkinseed populations in Türkiye and the rest of Europe. All four pumpkinseed populations collected in Türkiye clustered together, and their allelic composition appears to be most similar to fish from the lower Danube basin in Ukraine, i.e., a country located near Türkiye, and two populations in central Europe in the Czech Republic and Poland (Figure 1A). Unfortunately, our dataset did not include fish from Greece, which data might help confirm the primary source of pumpkinseed in Türkiye. Further successive separation of populations in the STRUCTURE analysis showed that Turkish populations grouped together and formed a separate cluster, indicating their strong genetic interrelationship (Figure 1B), which is in agreement with the suggestion of a single source for different localities in western Türkiye and Anatolia by Ağdamar et al. [21]. Interestingly, the population from Değirmenköy Reservoir, located in the European part of Istanbul, included specimens with different genetic origins, likely due to multiple introductions from various sources.

Based on the obtained results, the prediction that pumpkinseed populations with different haplotypes derived from a common European haplotype that is tolerant to a range of environmental conditions [21] would show low parasite diversity and abundance cannot be fully assessed. However, despite collecting fish of the common European haplotype, their parasite diversity appeared to be low in terms of parasites co-introduced along with the fish host and those acquired in the new environment. Similar results were found in pumpkinseed populations from Portugal and the Czech Republic, which exhibited low microsatellite allelic richness and heterozygosity [38], comparable to those in Türkiye. According to Luikart et al. [79], reduced heterozygosity may lead to increased parasite load in wild populations. However, this was not a general trend observed in our study, as most localities were inhabited by pumpkinseed with extremely low parasite abundance. Despite low heterozygosity and allelic richness, pumpkinseeds were rarely infected with local parasites. Moreover, except for the Sarıçay River, the infection by North American parasites was not high, reflecting their low availability in the environment, possibly due to the small founder population size with a limited number of North American parasites [52]. In addition to high environmental tolerance [21], low parasite load may thus be another trait of non-native pumpkinseed populations in Türkiye associated with rapid adaptation to new environmental conditions and establishment success, as was the case with pumpkinseed in the Sarıçay River [80].

Investigation of parasites in pumpkinseed in Türkiye has mainly focused on the European part of the country [81,82], with a single study from Asia focused on the rosette agent *Sphaerothecum destruens* Arkush, Mendoza, Adkison and Hedrick, 2003 in the Sarıçay River [83]. The previous studies [81,82] reported only 11 parasite taxa in pumpkinseed from Lake Sığırcı and Lake Gala, both located in the Meriç River basin. These taxa included monogeneans *Gyrodactylus* spp. and *Onchocleidus similis* (Mueller, 1936), metacercariae of *Clinostomum complanatum* (Rudolphi, 1814) Braun, 1899, *Diplostomum* sp., *Tetracotyle* sp., *Tylodelphys clavata* (von Nordmann, 1832) Diesing, 1850, acanthocephalan *Acanthocephalus* sp., nematodes *Eustrongylides excisus* Jägerskiöld, 1909 and Nematoda gen. sp., copepod *L. cyprinacaea*, and unidentified glochidia (summarised by [84]). Out of the parasite taxa previously found on pumpkinseed in Türkiye, just a single species, crustacean *L. cyprinacea*, was also found in this study. Our study identified at least seven additional parasite species infecting pumpkinseed in Türkiye, increasing the number of known parasite taxa associated with this fish species in the country. This finding suggests a richer parasite fauna in pumpkinseed populations than previously documented.

The co-introduction of parasites to new areas along with their hosts may be limited due to bottlenecks resulting from small founder populations [85]. Additionally, the probability of parasite co-introduction may depend on factors such as the host's origin (from low or high parasitised sources) or developmental stage (e.g., eggs, larvae, vs. adults; [52]). Our study confirms the presence of three North American parasite species in Türkiye: the

myxozoan *M. dechtiari*, the monogenean *O. dispar*, and the digenean *P. centrarchi*. These species were previously found in other European pumpkinseed populations (e.g., [38,45]). Notably, this study represents the first record of these North American parasite species in Türkiye; two (*O. dispar* and *P. centrarchi*) were observed in the Asian part of the country, while all three species were found in the European part. Interestingly, our study did not detect *O. similis*, previously found by Çolak [81] and Soylu [82] in lakes in the western part of the country. Dactylogyrid monogeneans are often host specific [86], and both *O. similis* and *O. dispar* primarily infect centrarchid fish [87]. The presence of different *Onchocleidus* species in both previous and current studies suggests potentially different sources of pumpkinseed for the localities in Gala and Sığırcı Lakes [81,82] and our sampling localities.

Onchocleidus dispar represents the most widespread and well-established co-introduced parasite in European pumpkinseed populations among the three species mentioned. Its presence in Europe dates back to the 1950s [88], making it one of the longest-known co-introduced parasites in pumpkinseed. Among the eight American monogeneans co-introduced to Europe [46,47], *O. dispar* represents the majority of single-species infections in many distant European populations. Records of single-species monogenean infection of pumpkinseed by *O. dispar* have been reported in various European regions, including south-west England [44], the basins of the Oder in Poland [36], the Dnieper in Ukraine [89,90], the Danube in the Czech Republic [38], and, in fact, the reservoirs on the Sado and Tejo rivers in Portugal [38]. Despite the high microsatellite similarity observed between pumpkinseed populations in Türkiye, indicating a common source of introduction, *O. dispar* was not observed in the Aegean region of Anatolia, specifically in the Sarıçay River and Dipsiz-Çine Stream. The absence of this parasite, which is specific for pumpkinseed and does not require other hosts in its life cycle, suggests either unfavourable environmental conditions for the parasite during or after pumpkinseed translocation or the introduction of very young or treated fish.

Posthodiplostomum centrarchi has recently been reported from various countries in Europe infecting both pumpkinseed and largemouth bass *Micropterus salmoides* (Lacepède, 1802) (e.g., [36,38,50,51,91], being distributed by its definitive hosts, herons (Ardeidae) [51]. Parasites collected in Sarıçay River and Değirmenköy Reservoir genetically corresponded to specimens obtained in Hungary and Portugal [50,92], as well as *Posthodiplostomum* sp. 3 sensu Locke et al., 2010, recovered from pumpkinseed in North America [93]. This study expands the distributional range of this non-native parasite to the Asian continent. Among the three North American parasites found, myxozoan *M. dechtiari* is the most recently observed, with only two reports from Europe. It was first observed in Hungary by Goswami et al. [45], and later, Kvach et al. [89] found it in the basin of the lower reach of the Danube River in Ukraine. This study marks the third report of this parasite in Europe.

The pumpkinseed in Türkiye harboured six parasite taxa, including one crustacean species, *L. cyprinacea*, and five taxa of larval nematodes. Most of these species occurred only occasionally, except for two relatively prevalent nematodes. *Paraquimperia tenerrima*, recorded solely in the Sarıçay River, was the most abundant parasite species, with a mean abundance of 6.6). In contrast, the mean abundance of other acquired parasites did not exceed one (see Table 4). This finding is also the first report of this parasite species in pumpkinseed. *Paraquimperia tenerrima* is a stenoxenous parasite known to infect the European eel (*Anguilla anguilla* L., 1758) as the definitive host, and it uses various fish species as paratenic hosts [94]. It is an indicator parasite of the eel populations, found mainly in old-age fish individuals [95]. Pumpkinseed, apparently susceptible paratenic hosts, had nearly 50% of individuals infected, with a maximum intensity of 70 larvae per fish. Further translocation of pumpkinseed infected with this parasite may spread *P. tenerrima* to other localities and subsequently infect local eel populations.

The second nematode parasite found in pumpkinseed with high prevalence (57%) were larvae of *Eustrongylides* sp. Despite primarily infecting fish-eating birds, larvae of *Eustrongylides* have zoonotic potential, being agents of human diseases [94]. Although rare, representatives of *Eustrongylides* have caused eustrongylidosis in humans in North

America, the Middle East, and Africa [96], potentially having socio-economic implications. Therefore, the continued expansion of non-native pumpkinseed populations in Türkiye poses a threat not only to natural conservation efforts and fisheries but also potentially to human health.

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Data Availability Statement: The data that support the findings of this study are available from the corresponding author, [M.O.], upon reasonable request.

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