

synthetic environments' on this planet or Mars!

What are your passions in life? I love science and arts as well as spending time in nature. I continue practicing ballet and enjoy climbing mountains (the Alps!).

What is it like being a scientist in Mexico? Being a scientist in Mexico requires a lot of endurance and creativity, as our politics and culture have yet to adopt science as a pillar for sustainable human and ecological development. Mexico now has its first woman (and a scientist!) as president! I am genuinely excited about this and hope that we can settle the basis for a long-term vision and commitment to science, human development, and sustainability (and I will continue to work in this direction too!).

What is your greatest research ambition? My most significant research ambitions at present are: firstly to understand arid ecosystems, which represent more than 40% of the world's surface area, to contribute to their sustainable use and conservation; secondly to mine the biotech potential of arid ecosystems (especially plants and their microbiomes) for social, sustainable, and innovative development; and thirdly to decipher microbial symbioses for the design of symbiotic systems that could interact with plants and animals in beneficial ways.

What is your advice for young scientists? If young people are curious and find joy and satisfaction in research, they are in the right place! They will need discipline, endurance, and imagination to find their way. Of course, I recommend that they search/find the right environment and mentors for their development. Science is a community effort, so building and being part of a good community are vital for science to flourish.

DECLARATION OF INTERESTS

The author declares no competing interests.

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Quick guide

Monogenean parasitic flatworms

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What are monogenean parasitic flatworms? In general, parasitic lifestyles, with their exploitation of host resources, necessitate profound evolutionary changes in behaviour, morphology, and genomes. Underlying patterns and mechanisms are fragmentarily understood at best. Monogenean parasitic flatworms are less publicly known or scientifically studied than helminths of well-known clinical concern, like tapeworms and flukes. Nonetheless, the World Register of Marine Species lists 5,706 accepted species of monogeneans in 76 families. These flatworms are mainly ectoparasites (infecting external body parts) of ectothermic aquatic vertebrates. Although several flatworm lineages live in or on a host, most flatworm species belong to a single clade, Neodermata, all representatives of which are parasites. Classically, next to the typically endoparasitic (i.e. living inside a host) tapeworms and flukes, most of which have a complex life cycle involving multiple host species, Monogenea is listed as a third neodermatan group, having a single-host life cycle.

This single-host life cycle is why monogeneans could thoroughly change our views on the acquisition of parasitism in flatworms. Recent phylogenomic work questioned whether endoparasitism arose only once in neodermatans and suggested that the single-host life cycle evolved on multiple occasions within neodermatan evolution, independently for monopisthocotyleans and polyopisthocotyleans (the two recognised monogenean groups), rendering "Monogenea" a non-natural (non-monophyletic) grouping (Figure 1A,B).

How long have we known about monogeneans? The first recognition of monogeneans as a group goes back

to the Belgian scientist Pierre-Joseph Van Beneden in 1858, using this terminology in view of the single-host life cycle. The first species discovered, now known as *Entobdella hippoglossi*, was described in 1776 by Otto Friedrich Müller and identified from halibut in an overview of Danish and Norwegian fauna. Considering it a leech, he called it *Hirudo hippoglossi*. It took time before monogeneans were discovered from other continents. Monogenean research in Africa started with the description of *Annulotrema gracile* in 1861, and in South America with that of *Benedenia hendorffii* in 1889. In North America, monogeneans seem to have been firstly reported from Canada in 1879 (*Octomacrum lanceatum*, *Polystomoidella oblonga* and *Sphyrnura osleri*), but were not reported from Central America before 1938. The first monogeneans described from Southeast Asia, in 1930, were *Dactylogyrus cyprini* and *D. puntii*, and from Australia in 1917 (*Encotyllabe pagrosomi*).

The quest for new species is far from over in monogenean research. A recent overview of records for new host-parasite combinations in the cichlid-infecting genera *Cichlidogyrus* and *Scutogyrus*, for instance, revealed that the discovery curve is still exponential, and that a limited number of researchers is responsible for these reports. When browsing NCBI GenBank for genomic resources of monopisthocotyleans and polyopisthocotyleans, a similar picture emerges: a few studies sometimes have a disproportionate influence. Indeed, the number of available genetic sequences is often not commensurate with the species richness of a genus nor with the research attention received on Web of Science.

Where do they occur? Monogeneans are the dominant ectoparasites of fishes. Teleosts, hagfishes, rays, and sharks harbour monopisthocotyleans (Figure 1D) on their skin or fins. Many species of polyopisthocotyleans (Figure 1C,E) and monopisthocotyleans (Figure 1F) infect fish gills.

We cannot talk biology without exceptions, and the niches occupied by monogeneans are more diverse than skin and gills. A minority of members of both recently proposed



taxa, Monopisthocotyla and Polyopisthocotyla, are endoparasites. Examples from the former are found in cichlid fishes' stomachs or urinary bladder, torpedo rays' hearts, and elasmobranchs' cloaca and rectal gland. Several polyopisthocotyleans have been reported in the urogenital system of herpetiles, while others infect hippopotamus eyes or inhabit the mouth and gills of Australian lungfish.

An interesting debate regarding host use surrounds monogeneans on fish-infecting parasitic crustaceans, as they may be living on the crustacean while feeding on the fish, rather than parasitising on the parasitic crustaceans. In Monopisthocotyla, this phenomenon is most common in udonellids, and in Polyopisthocotyla, in diclidophorids. Other monopisthocotyleans found on invertebrates are the various *Isancistrum* species, which parasitise squids. Also, one of the most species-rich helminth genera worldwide, *Gyrodactylus* (like *Isancistrum*, belonging to the gyrodactylids), includes some species infecting amphibians, but mainly species living on a broad array of fishes. They sometimes show pronounced specificity to certain infection sites, such as (parts of the) skin, fins, head, or gills. The ecologically and geographically broad distribution of representatives of this genus nicely illustrates the diversity of aquatic habitats in which monogeneans and their hosts occur: from Antarctic cod icefishes to the Okavango Delta. This broad niche is also demonstrated by the impressive tolerance of several members to certain physicochemical conditions. This is true at the species level; for example, some monogeneans infecting goby fishes occur on several hosts in localities of substantially different salinity along the North Sea, western Mediterranean and Adriatic coasts. It also holds true at the population level, exemplified by species living in highly variable and sometimes extreme salinity, such as northern Italian pools, the alkaline soda lake Lake Magadi in Kenya, and the intertidal and supratidal zones of a Chilean rocky shore. This is in contrast to other monogeneans, which have a tolerance to salinity change that is remarkably lower than that of their euryhaline host, e.g. *Cichlidogyrus* spp. from blackchin

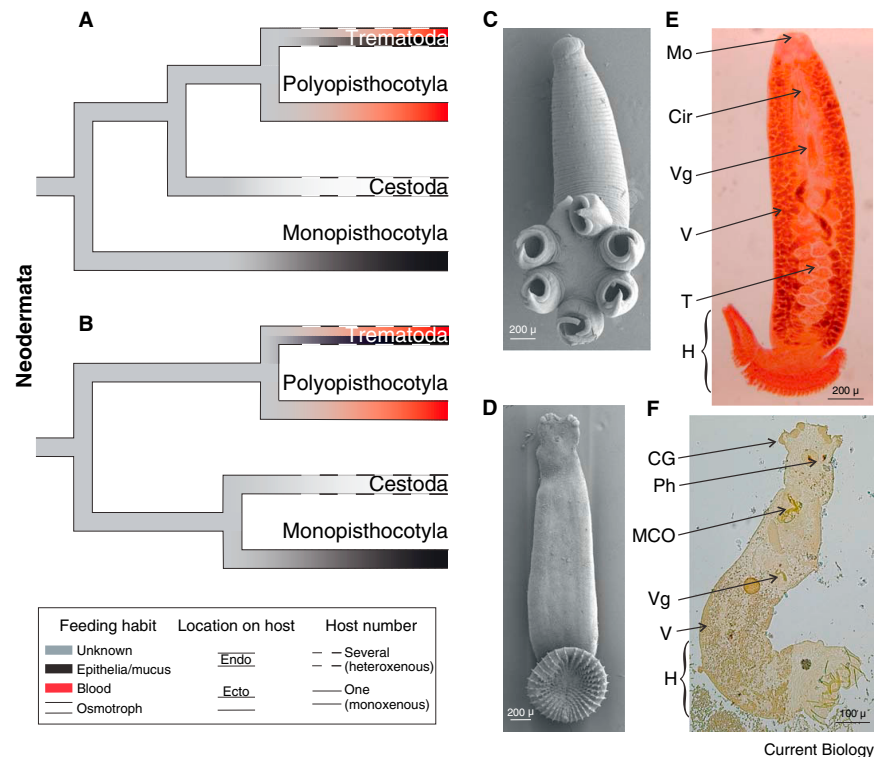


Figure 1. Evolutionary scenarios, examples of monogeneans and their morphology.

(A, B) Alternative hypotheses regarding the phylogeny of neodermatan flatworms, with main feeding mode, location on the host, and number of hosts in the life cycle indicated for each group. In both recently remaining scenarios, monogeneans do not form a monophyletic group. (C) *Rajonchocotyle emarginata* (Polyopisthocotyla, Hexabothriidae): scanning electron microscopy image used with permission from N. Kmentová. (D) *Acanthocotyle verrilli* (Monopisthocotyla, Acanthocotylidae): scanning electron microscopy image used with permission from N. Kmentová. (E, F) Typical examples of monogenean whole mounts for morphological characterization. (E) *Pyragraphorus hollisae* (Polyopisthocotyla, Pyragraphoridae): light micrograph from a carmine stained specimen mounted in Canada balsam, image used with permission from W. Boeger. (F) *Cichlidogyrus bilongi* (Monopisthocotyla, Dactylogyridae): light micrograph from a specimen mounted in glycerin ammonium picrate, image used with permission from A. Pariselle. CG, cephalic glands; Cir, cirrus; H, haptor (posterior attachment organ: in this case Monopisthocotyla with seven pairs of hooks, two pairs of anchors and two bars; Polyopisthocotyla with numerous clamps); MCO, male copulatory organ; Mo, mouth; Ph, pharynx; T, testicles; V, vitellogenic glands; Vg, vagina.

tilapia. Another ‘extreme’ environment hosting monogeneans is the deep sea.

Granted, they are ubiquitous, but otherwise aren’t all helminths the same? Simple as it may be, the single-host life cycle is what sets “Monogenea” apart from most other parasitic flatworms and from many other helminths. While this direct life cycle without intermediate hosts is also found in many other ectoparasites (e.g., parasitic crustaceans), other aspects of the life history of some monogeneans are unique among animals. Examples include diplozoids (Polyopisthocotyla), where two individuals coalesce, grow together as they mature, then stay in cross-copulation until the end

of their days. And in gyrodactylids (Monopisthocotyla), the viviparous representatives have significantly shortened life cycles and give birth to fully grown young with already developing embryos, a reproductive strategy named hyperviviparity.

They are parasites, so how worried should I be? Monogeneans do not pose risks to humans. They have been intensely studied as potential disease agents in fisheries and aquaculture, where their negative effects (of other than solely scientific interest) are most well known. Controlled conditions with often high fish densities facilitate monogenean transmission and proliferation, causing higher parasite

abundance. Under these artificial conditions, monogeneans provoke a breakdown of immunological barriers and can therefore act as gateways of secondary infections (such as by bacteria and fungi). Examples of such threats to marine aquaculture are species of *Neobenedenia* (Monopisthocotyla), generalist parasites with global occurrence. *Gyrodactylus salaris* (Monopisthocotyla), the ‘salmon killer’, invoked national measures aimed at its eradication in Norway. While the eradication programme has been officially proclaimed as highly successful, ten rivers remain affected. *G. salaris* can cause up to 100% mortality of farmed Atlantic salmon and, more importantly, 98% mortality in wild populations. Given that a non-native parasite strain is the causative agent, the drastic impact of *G. salaris* under natural conditions showcases the fragility of host–parasite interactions in the face of anthropogenic disturbances such as biological invasion, rather than the threat of monogeneans under natural circumstances. Evaluation of parasite invasion potential is often overlooked in fish trade and host conservation efforts. However, the overall importance of parasites including monogeneans in the food web is well-recognised. In addition, the significance of parasites as part of balanced ecosystems has been recently highlighted in the mission of the IUCN Species Survival Commission Parasite Specialist Group.

Why should I also start studying these flatworms?

The high degree of species richness of monogeneans, often with several species known per host species, offers a considerable dataset of helminths to study. The above-mentioned *Gyrodactylus* was even coined the *Drosophila* of the parasitic world. Its representatives infecting hosts such as salmonids, guppies, and gobies are quite well-studied in terms of genomics, host colonisation, and parasite speciation.

Indeed, with their diversity and life cycles, and apparently even some well-studied host–monogenean systems as candidate models — for example, for epidemiology, developmental biology, and molecular, ecological, and evolutionary parasitology — what’s not to like about monogeneans, and why are these fascinating helminths

not under greater scientific scrutiny? Monogeneans typically range in length from a couple of tenths of a millimetre to one or even some centimetres; the megadiverse families Gyrodactylidae (more than 600 species) and Dactylogyridae (more than 1,000 species) mainly consist of representatives less than 1.5 millimetres in length. To the untrained hand, their often minute size causes technical challenges regarding finding, observing, manipulating, and storing these animals, and especially for obtaining sufficient high-quality material for -omics approaches. The fundamentally different and highly divergent architecture of flatworm genomes in comparison to those of most other metazoans makes it difficult to apply commonly used molecular methodology to monogeneans.

On the bright side, by virtue of their single-host life cycle, there are fewer confounding factors than with multi-host life cycles when studying the fundamentals of a parasitic lifestyle, such as how host biology or the environment influences parasites. Therefore, we could not agree more with proposals of monogeneans as models in ecological and evolutionary parasitology. Changes in their communities may have a sentinel function for human impacts on the ecosystem, as recently suggested in Lake Victoria. They may serve as excellent ‘tags’ for the history, biogeography, or ecology of their host. For example, members of *Macrogyrodactylus* have been used to infer the historical distribution of catfishes, while dactylogyrid monogeneans infecting cichlid fishes can help reconstruct the origins of their hosts, in terms of intercontinental biogeography and the source of anthropogenically introduced stocks. The life cycle also offers advantages for maintaining host–monogenean systems in the laboratory; this has rendered the sole-infecting *Entobdella soleae* a model for colonisation of, and attachment to, fish skin.

Where can I find out more?

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DECLARATION OF INTERESTS

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