

SCALE BAR: 10µm

Monogenean parasites of fishes have remarkable adaptations to parasitism, but according to **Dr Graham Kearn** these fascinating organisms are virtually unknown to naturalists

MONOGENEANS THE ULTIMATE FISH PARASITES

MAIN IMAGE, LEFT

Fig. 4. A lateral view of the haptor of *Tetraonchus monenteron* from pike gills, showing one of the two lateral pairs of large hooks that impale the gill leaflets by counter-rotation. Photo: Richard Evans-Gowing by scanning electron microscope. Scale bar: 10µm. Reproduced from Kearn (2004) with kind permission of Springer Science and Business Media. © Springer 2004



Anyone who has gone pond-dipping will be familiar with planarians. They glide with no apparent effort across the substrate, propelled as if on a magic carpet by microscopic motile hairs (cilia). Planarians are flatworms (platyhelminths) and are free-living (non-parasitic), but many of their relatives have embarked on a parasitic lifestyle. Some of us may recall from our school days the complex life cycles of other parasitic flatworms, the pork tapeworm, *Taenia solium*, and the sheep liver fluke, *Fasciola hepatica*. Few, however, are familiar with monogeneans, despite the fact that most common fishes harbour one or more species of these parasites (Table 1, page 34).

As summarised by Kearn (1998, 2004) most monogeneans live on the skin (Fig. 1) or gills of fishes and many are host specific, i.e. each monogenean species is restricted to a single, or to one or two closely related fish species (Table 1). The consequence of this phenomenon is that, following a cursory examination of a detached parasite in the absence of the host, a specialist is often able to name the host fish.

Life cycles of tapeworms and flukes involve at least two hosts, but monogeneans have relatively simple cycles with only one host. They spread directly from fish to fish either by way of freely swimming larvae (oncomiracidia) propelled by cilia, or by contagion, adult or juvenile parasites transferring between fishes when they make contact. Others infect Chelonian reptiles (terrapins).

Table 1 (page 32) shows a selection of common British marine and freshwater fishes and their monogenean parasites. Marine hosts include sharks and rays (cartilaginous fishes or

BIOGRAPHY



Dr Graham Kearn was awarded the degree of D.Sc (University of Birmingham) in 1974 and was visiting fellow in the Department of Parasitology, University of Queensland, Australia in 1975-1976 and again in 1990-1991, and the Seto Marine Biological Laboratory, University of Kyoto, Japan in 1990. He is the author of more than 130 research papers and review articles and two books.

elasmobranchs) as well as bony fishes (teleosts). One of the largest monogeneans, measuring up to 2cm in length, is *Entobdella hippoglossi* from the skin of the halibut. It was also the first monogenean to be recorded, by Müller in 1776, but a satisfactory description was not published until 1858 by Van Beneden, whose excellent illustration is reproduced in Fig. 2.

A surprising recent discovery is that Atlantic halibut hosts a second species of *Entobdella* (Kearn *et al.* 2007). This parasite, named *Entobdella vanbenedeni*, is as big as, sometimes bigger than, *E. hippoglossi*. The two parasites are superficially similar, but careful comparison reveals consistent differences in anatomical detail that have gone unrecognised since the 18th century.

Two groups of monogeneans make an especially large contribution to our freshwater fauna. These are dactylogyrids, gill parasites that have speciated extensively on fish of the carp family (Cyprinidae), and gyrodactylids, found on the skin and gills of many of our freshwater fishes and also on some marine hosts. Dactylogyrids and gyrodactylids lie at the other

end of the size spectrum from *E. hippoglossi*, ranging in length from 0.5 to 2mm.

A monogenean lives in the bladder of our common frog, *Rana temporaria*, and others infect chelonian reptiles (terrapins). Another occurs in what seems a most unlikely habitat, beneath the eyelids of the hippopotamus.

Attachment

Gill parasites are continually exposed to strong gill-ventilating currents generated by their fish hosts. On occasions when particulate

material or pollution enters the gill chamber, parasites may also be subjected by their hosts to 'coughing' pulses, in which the strength of the water flow may be suddenly and briefly increased and its direction temporarily changed. Thus a parasite must at all times attach itself securely to the gills and be capable of resisting the extra stresses generated during 'coughing' episodes. It might be thought that attachment to fish skin would be less challenging, especially if the host is a flatfish or a fish that spends part of the day resting. However, flatfishes are capable of sudden bursts of speed and attachment organs of skin parasites must meet these challenges.

Hooks are the 'hallmark' of monogeneans. These elegantly shaped structures (Fig. 3) occur at the posterior end of the body on a muscular, often disc-shaped attachment organ called the haptor (Fig. 2). Hooks are of two sizes: up to 16 tiny hooklets, ranging in length from about 7 to 40 µm, arranged radially on the haptor disc, and one or two pairs of more massive hooks (Fig. 4), which may reach 0.5mm in length. The hooklets mainly serve to pin the small larva to the delicate outer layer of cells (epidermis) of the host's skin, while the larger hooks may pass through the epidermis into the thicker and tougher inner layer of the skin or dermis, providing anchorage for the much larger adult parasites.

“ Marine hosts include sharks and rays as well as bony fish ”



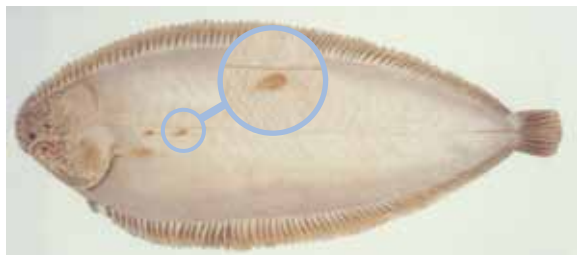


Fig. 1. The lower surface of a common sole (*Solea solea*) infected by two adult specimens of the monogenean *Entobdella soleae*. Colour lithograph from a water-colour by Annie Willis in Cunningham, 1890.

Fig. 2. An early drawing by Van Beneden (1858) of *Entobdella hippoglossi* – the first monogenean to be described. Note posterior, saucer-shaped sucker (haptor) with embedded hooks.

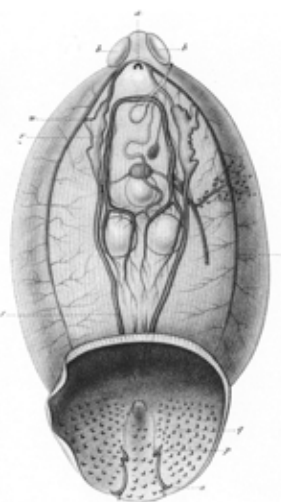


Fig. 3. A variety of monogenean hooks (not to scale).

For Fig. 4 see main image page 28

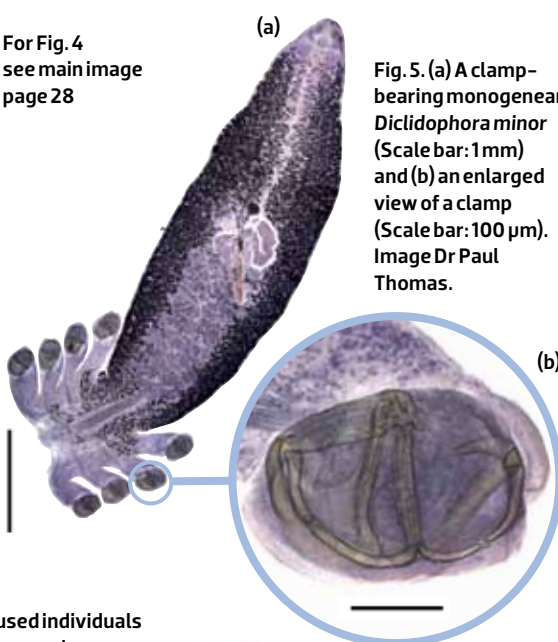


Fig. 5. (a) A clamp-bearing monogenean, *Dicliphora minor* (Scale bar: 1 mm) and (b) an enlarged view of a clamp (Scale bar: 100 µm). Image Dr Paul Thomas.



Fig. 6. *Pseudaxine trachuri*, an asymmetrical clamp-bearing gill parasite. Note brown or black pigment (haematin) derived from ingested host blood. Scale bar: 500 µm. Image Dr Paul Thomas.

Fig. 7. Two fused individuals of *Diplozoon paradoxum*. Scale bar: 1 mm. Image Dr Paul Thomas.

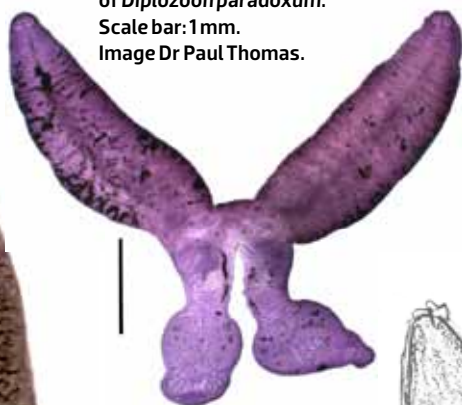


Fig. 8. A living larva of *Entobdella soleae*.



Fig. 9. An adult *Polystoma integerrimum* from the bladder of a common frog. Scale bar: 1 mm. Specimen donated by Professor Richard Tinsley. Image Dr Paul Thomas.

Some skin parasites like *Entobdella* use movements of the large hooks embedded in the haptor to generate suction. The gill parasite *Tetraonchus* uses counter-rotation of its two lateral pairs of large hooks (Fig. 4) to impale the bases of two adjacent gill leaflets (the tiny flaps that contain blood and extract oxygen from the gill-ventilating current).

But it is among the gill parasites of bony fishes that bio-engineering has reached an exceptional level. Some of these lowly flatworms have developed three or four pairs of clamps, each with two opposable semi-circular jaws capable of grasping one or two gill leaflets (Fig. 5). Some of these gill parasites are asymmetrical. For example *Pseudaxine trachuri* on horse mackerel, *Trachurus trachurus*, has 25 or more clamps on one side of the body (Fig. 6). The parasite must possess a surprisingly sophisticated sensory/motor system to co-ordinate the operation of these clamps.

The sizes of *Tetraonchus* and related parasites are limited by the need to fit between two adjacent gill leaflets, but no such restriction applies to the clamp-bearing parasites and many of them are large, from 0.5 to 1 cm long (Figs. 5–7).

Feeding

Skin parasitic monogeneans like *Entobdella soleae* feed on host epidermal cells. A large protrusible glandular pharynx is used to erode and ingest host epidermis. Monogeneans have no blood system and intestinal branches transport nutrients to remote parts of the body. The parasites exploit the wound healing properties of host epidermal cells, which migrate from the edge of the feeding wound and repair the lesion. Damage inflicted at a single feeding site by *E. soleae* probably heals within 24 hours. Damage to the host in the wild is therefore minimal, but this is not the case in fish farms and aquaria.

Gill parasites like *Tetraonchus* also feed on epidermis but the larger clamp-bearing gill parasites like *Dicliphora* and *Pseudaxine* ingest blood, as indicated by intestinal deposits of the indigestible brown or black pigment haematin derived from host haemoglobin (Fig. 6).

Locomotion and mating

All monogeneans, with the exception of clamp-bearing monogeneans, are

capable of moving from place to place on the host in the manner of a leech. *E. soleae* has adhesive glandular pads on the head that are used for temporary attachment when the parasite changes the location of its haptor. Two secreted components are thought to interact like an epoxy-resin to attach the head to fish skin (Kearn & Evans-Gowing 1998). This cement is remarkable in that fish skin is wet and slimy and yet the bond is very strong. When the locomotion step is completed and the haptor reattached, the parasite can break the adhesive bond instantly.

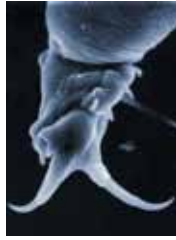
There is no need for monogeneans to move to find food since, whether their diet is epidermis or blood, it is a renewable resource that is always within reach. It is more likely that locomotion creates opportunities for sperm exchange between the hermaphrodite adults. Some monogeneans, like *Entobdella*, exchange spermatophores (packages containing sperm) and some, like *Diclidophora merlangi*, use 'hypodermic impregnation'. Others mate in the conventional way. Adult clamp-bearing monogeneans have become sedentary, posing the question of how sperm exchange is achieved. We know little about their reproductive biology but some adults, like *Diclidophora merlangi*, tend to cluster on the gills and individuals are sufficiently extensible to make contact with each other.

The freshwater gill parasite *Diplozoon paradoxum* goes further: two individuals fuse so that their reproductive ducts communicate permanently (Fig. 7). This unique and remarkable development is reflected in the name 'Diplozoon', meaning 'double animal'.

It is advantageous for a sedentary parasite to interact as little as possible with host gill flow to reduce the risk of dislodgement and interference with host gaseous exchange. This requires streamlining of the body of the parasite. Since many of these parasites are exposed to a unilateral water current, streamlining can only be achieved by adopting an asymmetrical shape (Fig. 6). Clamps on one side of the body are attached upstream and those on the other side of the body are lost.

Finding a host

With the exception of gyrodactylids, which give birth to living young,



monogeneans lay eggs. These eggs have shells made of a tough protein called sclerotin and are released into the sea, lake or river. The larva, usually ciliated, embryonates inside the egg. A detachable lid or operculum permits the larva to escape into water where it is propelled by beating cilia. This tiny larva is only 0.25 mm long in *Entobdella soleae*, just visible to the naked eye (Fig. 8), and has the task of locating and attaching itself to the host. Since most monogeneans are specific to only one or two closely related hosts, this is a very demanding task.

We know more about how this is achieved in *E. soleae* than in any other monogenean. Its host, the common sole, is a nocturnally active flatfish that spends the daylight hours partly buried in sediment at the sea bed. Adult parasites are typically found on the unpigmented lower surface of the sole (Fig. 1). The eggs of the parasite hatch at dawn or soon after and the larvae have all the hours of daylight to make contact with a resting sole. Each day, while fully embryonated eggs are still available, small numbers of larvae will emerge at dawn, thereby spreading hatching over a period of days to maximise the chances of some of them meeting a resting sole. But the parasite has a second option. If a sole should settle near fully embryonated parasite eggs, an unknown chemical (or chemicals) in the mucus stimulates hatching within 5 minutes, with every chance that the newly released larvae will establish themselves on the host that provided the stimulus. Once attached by the haptor and its ring of hooklets, the cells bearing cilia that enabled the larva to swim are jettisoned. Larvae of *E. soleae* rarely attach to other flatfish species and this strong selective ability seems to have a chemical basis.

Many other monogeneans have rhythmical hatching patterns, but chemical stimulation of hatching has gone further in species of *Acanthocotyle* living on the skin of rays. The larvae of *Acanthocotyle* are unable to swim (they have no cilia) and fail to hatch spontaneously. If a host ray settles on top of the eggs on the sea bottom, ray mucus induces hatching in seconds. The larva does not need to swim since by greatly elongating its body the lower skin of the resting host can usually be

reached by its anterior adhesive pads. In this case the identity of the chemical hatching stimulus is known – it is urea, a waste product of protein metabolism that is retained in the bodies of sharks and rays and has an important role in water balance. Because of this quirk of physiology, urea is present in relatively large quantities in elasmobranch skin secretions and *Acanthocotyle* has exploited this unusual metabolic feature for host location.

Unhatched larvae of other species respond to different host-derived cues. The eggs of the skin parasite *Neoentobdella diadema* hatch within seconds in response to shadows cast by cruising or resting stingrays. Eggs of the gill parasite *Diclidophora luscae* are stimulated to hatch by disturbance created as their fish hosts (pouting, *Trisopterus luscus*) forage.

The viviparous gyrodactylids have no cilia and parasites transfer either directly to new hosts when fishes make contact or by way of the substrate as a staging post (Bakke *et al.* 2007).

Polystoma and the common frog

We have only one native monogenean parasitising amphibians in Britain, namely *Polystoma integerrimum* (Fig. 9). It is a relative of the clamp-bearing gill parasites of fishes but inhabits the bladder of the common frog *Rana temporaria*, where it attaches, not by clamps, but by three pairs of haptor suckers. A link with the clamp-bearers is provided by its diet, which is blood extracted from blood vessels in the bladder wall.

The common frog spends most of its time on land, entering water for just a few weeks in the spring to breed. Like most other monogeneans, *Polystoma* has a free-swimming ciliated larva and egg production and egg laying are restricted to the spring period spent by the frog in water.

The larvae attach themselves not to the adult frog but to the gills of the tadpole, providing another link to the gill parasites of fishes. They remain on the gills of the tadpole until host metamorphosis takes place and the young frog leaves the water. At this time the larvae leave the gills and migrate to the bladder where they reach sexual maturity and spend the rest of their lives. Host hormones

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circulating in blood and accessible to the parasites in their diet may switch on egg production in the adult parasite and migration of larval parasites at host metamorphosis.

Host/parasite co-evolution

Amphibians may have inherited monogeneans like *P. integerrimum* from their fish ancestors by a process of co-evolution. As the hosts evolved and speciated, their parasites correspondingly speciated, leading to a congruence between lineages of host and parasite. On the other hand, amphibians could have acquired their monogeneans by host switching, in which a parasite transfers from one host (a freshwater fish) to an unrelated host (an amphibian) sharing the same environment. It is not easy to determine which of these two mechanisms was involved. However, there can be no doubt that the parasite living beneath the eyelids of the hippopotamus reached this surprising habitat by host switching, since it is closely related to frog parasites and is the only monogenean parasitising a mammal. Its name – *Oculotrema hippopotami* – indicates its host and its strange habitat.

A fascinating fact is that each major group of fish-like vertebrates has its own special group of blood-feeding monogenean gill parasites. We have met just one of these parasite groups, the clamp-bearers parasitising the bony fishes. The implication is that ancestral blood-feeding monogeneans may have been present on the ancestors of the fish-like vertebrates before these early vertebrates diverged, perhaps as far back as the Ordovician period (approximately 490 to 440 million years ago). This makes the dinosaurs look modern.

In spite of their hooks, clamps and suckers and their feeding activities, monogeneans have little impact on their hosts in the wild. About half the soles in the North Sea are infected by *Entobdella soleae* and infected

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TABLE 1
A selection of common British fishes and their monogenean parasites.

individuals rarely carry more than two or three relatively small adult parasites, each up to 5 or 6 mm in length (Fig. 1).

Threats from monogeneans

However, in aquaria the populations of parasites on captive soles increase rapidly, since invasion success of their free-swimming larvae is much higher than in the open sea. There is a margin of safety because captive soles can support two or three dozen adult parasites with no obvious ill effects. But the host seems incapable of preventing further population increase and unless the sole is treated (freshwater kills marine monogeneans rapidly), the parasite burden will increase exponentially and host epidermis will be removed faster than the host can replace it. The osmotic (water) balance of affected fishes will be seriously impaired and pathogenic micro-organisms may gain entry, leading ultimately to death. Thus

monogeneans can pose a real threat in situations where fish are confined as in fish farms and public aquaria.

Gyrodactylid monogeneans give birth to unciliated adults that establish themselves on the same host individual (autoinfection). As a result, they avoid the mortality to which free-swimming larvae are subjected and populations on individual hosts initially increase rapidly, even in the wild. However, many hosts are able to limit this expansion and may even eliminate the infection by mechanisms that are not yet fully understood (Bakke *et al.* 2007). Hosts unable to limit parasite numbers are unlikely to survive. For example, *Gyrodactylus salaris* is notorious as a killer of freshwater salmon parr (*Salmo salar*) in Norway, not just in fish farms but also in the wild, although brown trout (*Salmo trutta*) are able to control the parasite. Britain is currently free of *G. salaris*.

More reading and references at www.societyofbiology.org/biologist

Host common name	Host scientific name	Parasite	Where
Marine			
Common (Dover) sole	<i>Solea solea</i>	<i>Entobdella soleae</i>	Skin
Atlantic halibut	<i>Hippoglossus</i>	<i>Entobdella hippoglossi</i>	Skin
	<i>Hippoglossus</i>	<i>Entobdella vanbenedeni</i>	Skin
Mackerel	<i>Scomber scombrus</i>	<i>Kuhnia scomбри</i>	Gills
		<i>Kuhnia sprostonae</i>	Gills
		<i>Grubea cochlear</i>	Gills
Whiting	<i>Merlangius merlangus</i>	<i>Diclidophora merlangi</i>	Gills
Pouting	<i>Trisopterus luscus</i>	<i>Diclidophora luscae</i>	Gills
Blue whiting	<i>Micromesistius poulassou</i>	<i>Diclidophora minor</i>	Gills
Red gurnard	<i>Aspitrigla cuculus</i>	<i>Plectanocotyle gurnardi</i>	Gills
Grey gurnard	<i>Eutrigla gurnardus</i>	<i>Plectanocotyle gurnardi</i>	Gills
Tub gurnard	<i>Trigla lucerna</i>	<i>Plectanocotyle gurnardi</i>	Gills
Horse mackerel	<i>Trachurus trachurus</i>	<i>Gastrocotyle trachuri</i>	Gills
		<i>Pseudaxine trachuri</i>	Gills
Dogfish	<i>Scyliorhinus canicula</i>	<i>Leptocotyle minor</i>	Skin
Roker (Thornback ray)	<i>Raja clavata</i>	<i>Acanthocotyle lobianchi</i>	Skin
Stingray	<i>Dasyatis pastinaca</i>	<i>Neontobdella diadema</i>	Skin
Freshwater			
Pike	<i>Esox lucius</i>	<i>Tetraonchus monenteron</i>	Gills
Grayling	<i>Thymallus thymallus</i>	<i>Tetraonchus borealis</i>	Gills
Brown trout	<i>Salmo trutta</i>	<i>Discocotyle sagittata</i>	Gills
Rainbow trout	<i>Oncorhynchus mykiss</i>	<i>Discocotyle sagittata</i>	Gills
Bream	<i>Abramis brama</i>	<i>Diplozoon paradoxum</i>	Gills
		<i>Dactylogyrus auriculatus</i>	Gills
3-spined stickleback	<i>Gasterosteus aculeatus</i>	<i>Gyrodactylus gasterostei</i>	Skin
9-spined stickleback	<i>Pungitius pungitius</i>	<i>Gyrodactylus pungitii</i>	Skin
Roach	<i>Rutilus rutilus</i>	<i>Neodactylogyrus crucifer</i>	Gills

