# Some Aspects of the Biology of Monogenean (Platyhelminth) Parasites of Marine and Freshwater Fishes

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Müller [1] was the first to describe a monogenean, collected from the skin of the halibut (*Hippoglossus hippoglossus*). However, he regarded the parasite as a leech and named it *Hirudo hippoglossi*. It was not until 1858 that its status as a monogenean was established by van Beneden [2] and named *Epibdella* (now *Entobdella*) *hippoglossi*. Van Beneden published a detailed and accurate description of the parasite and one of his excellent illustrations is reproduced here in Figure 1. *Entobdella hippoglossi* is one of the largest monogeneans, measuring up to 2 cm in length. It has a smaller relative, measuring 5 to 6 mm in length, which was described by van Beneden and Hesse in 1864 [3] and named *Phyllonella* (now *Entobdella*) *soleae* from the skin of the Dover or common sole, *Solea solea* (Figures 2 and 3). This parasite is now perhaps the best known monogenean in terms of its biology [4-6].

The Phylum Platyhelminthes (flatworms) to which the Monogenea belongs is a major sub-division of the Animal Kingdom. Platyhelminths lack a skeleton and a blood system and are regarded as relatively simple on an evolutionary scale of anatomical development, just 'ahead' of sponges and cnidarians. Many flatworms are free-living but they also include three groups with parasitic life styles. Two of these, the Cestoda (tapeworms) and Digenea (flukes) parasitise the full range of vertebrates, from fishes to mammals, and have complex life cycles, with one or two intermediate hosts in addition to the main or definitive vertebrate host [4]. Members of the third parasitic group, the Monogenea, are mostly restricted to the skin and gills of marine and freshwater fishes and have relatively simple life cycles, lacking intermediate hosts, new hosts being infected by tiny free-swimming ciliated larvae or oncomiracidia (Figures 3 and 4). Exceptions to this are the gyrodactylid monogeneans (Figure 5B), most of which are viviparous (some are oviparous as are most monogeneans), giving birth to unciliated individuals similar
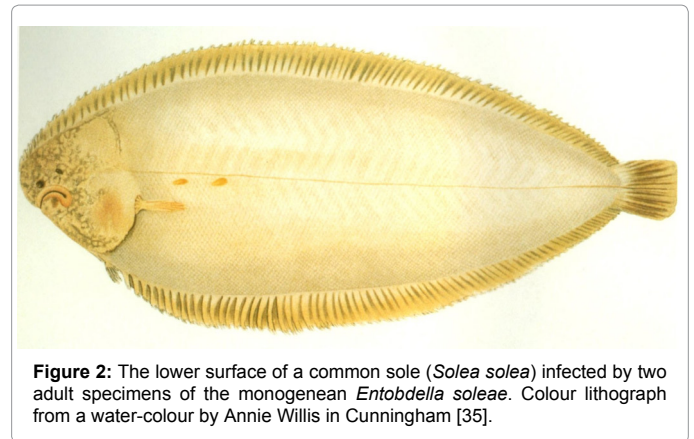


**Figure 1:** An early drawing by van Beneden [2] of *Entobdella hippoglossi* in ventral view.



**Figure 2:** 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 [35].

in size to the parent [4,5]. These parasites spread to new hosts by contagion, via the substrate as a staging post, by contact with detached drifting parasites or by contact between living fishes and infected dead fishes [7].

An outline classification of the Monogenea, showing the relationships of the families is available in Kearn [5], although aspects of this scheme are controversial.

Every major group of fish-like vertebrates is parasitised by monogeneans. They have been recorded on 'primitive' jawless agnathans, on holocephalans, on the coelacanth, *Latimeria chalumnae*, and on sturgeons [5]. Monogeneans are widespread on sharks and rays (elasmobranchs) and polystomatid monogeneans have colonised tetrapods, including frogs (anurans), freshwater turtles (chelonians), and, surprisingly, one mammal, the hippopotamus [8,9]. However, monogeneans achieve their greatest diversity on the bony fishes (teleosts) and especially the freshwater cyprinid fishes. The 'explosive' radiation of the cyprinids is matched by two genera of freshwater monogeneans that rely on hooks for attachment, namely *Dactylogyrus* on the gills (Figure 5A), with more than 900 species worldwide [10] and *Gyrodactylus* on the skin and gills (Figure 5B), with 402 described species, according to Bakke, et al. [11]. *Dactylogyrus* spp. are highly diverse, much of this diversity associated with the copulatory
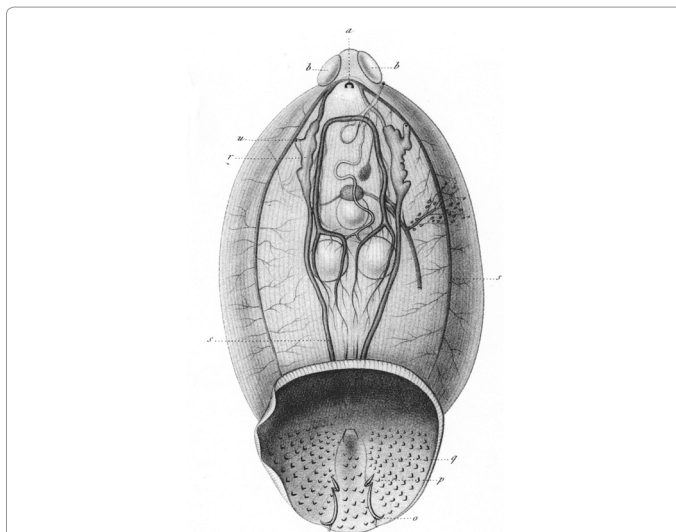
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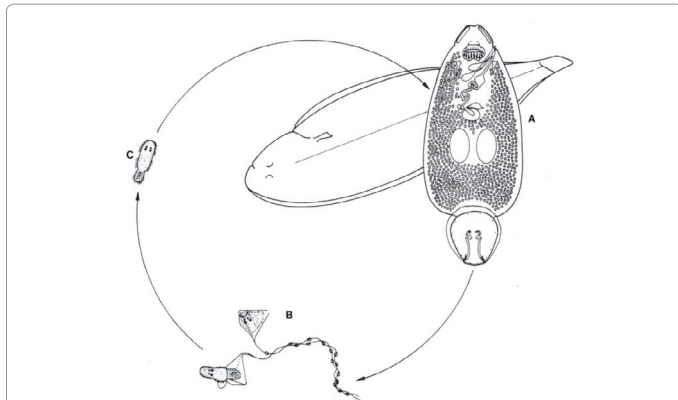
**Figure 3:** The life cycle of *Entobdella soleae*. The adult parasite (A) inhabits the lower surface of the common sole (*Solea solea*). Tetrahedral eggs attached to sand ballast on the sea bed (B) liberate free-swimming, ciliated larvae (oncomiracidia) (C), which typically invade the upper surface of the sole and migrate to the lower surface. From Kearn [5].
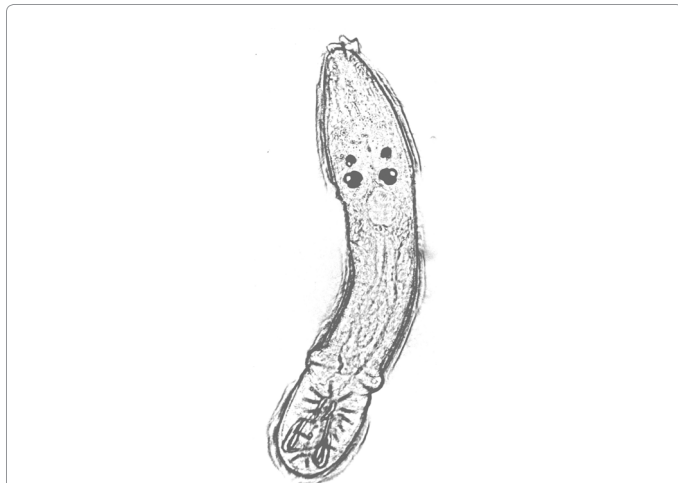


**Figure 4:** A living larva of *Entobdella soleae*. Length is about 250 μm. From Kearn [6]. Reproduced with permission from The Society of Biology.
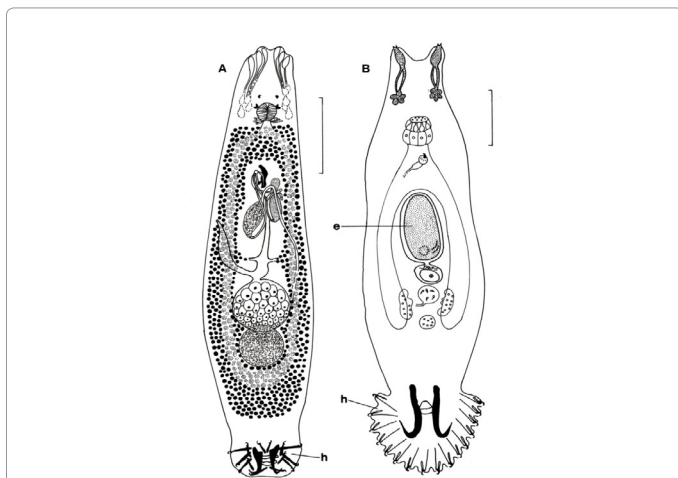


**Figure 5:** A: *Dactylogyrus squaliobarbi*, an oviparous monogenean. B: *Gyrodactylus pungitii*, a viviparous monogenean. Modified from (A) Gusev [36] and (B) Malmberg [37]. e, Embryo; h, haptor. Scale bars 100 μm.

apparatus. In contrast, the morphology of gyrodactylids is remarkably conservative [12].

Compared with other vertebrates, fishes have unique anatomical features that have been extensively exploited by parasitic animals and in particular by monogeneans. The first of these features concerns the skin. Like other vertebrates the skin of fishes consists of an outer epidermis and an inner dermis, but unlike mammals, fish epidermis consists of ten or more layers of living epidermal cells, with cell division taking place throughout, most commonly in the deeper layers [5]. In mammals the outer layer of epidermal cells dies, producing a cornified protective layer, difficult for a parasite to digest. Thus, fish epidermis is a readily accessible and nutritious food for a skin parasite. In addition, epidermis has an important role in wound healing and this is exploited by skin-parasitic monogeneans. When the epidermis is damaged the neighbouring epidermal cells multiply and migrate, sealing skin lesions quickly and effectively. Circular skin wounds of the size made during feeding by *Entobdella soleae* are likely to be repaired rapidly.

*E. soleae* has no jaws or teeth and relies on secretion from a large glandular pharynx to dislodge and perhaps partially digest superficial host epidermal cells [13]. There are blood vessels in the dermis but not in the sole's epidermis, so the gut contents of the recently-fed parasite are colourless. In the sole and in other bony fishes there are bony scales secreted by and located in the superficial layers of the dermis, but sole scales do not interfere with epidermal grazing because the exposed surfaces of the scales are covered by epidermis.

It might be supposed that the water currents to which skin-parasitic monogeneans are exposed are relatively weak and even temporarily absent in fishes like the common sole, which spends long periods at rest on the bottom. However, many fishes, including flatfishes, are capable of generating sudden bursts of speed and the attachment organs of their skin parasites must be capable of resisting dislodgement. Hooks are the 'hallmark' of monogeneans, occurring at the posterior end of the body on a muscular attachment organ or haptor (Figures 1, 3 and 5). Hooks come in two sizes: up to 16 tiny hooklets (14 in *Entobdella*), between 7 and 40 μm in length, and one or two pairs of much larger hooks, sometimes reaching 0.5 mm in length. The tiny hooklets are essentially larval structures, used to pin the small larva to the delicate outer layer of host epidermal cells [14], but they persist in adult *Entobdella* spp. around the edge of the saucer-shaped haptor. The larger hooks may pass through the epidermis and provide anchorage for the much larger adults in the thicker and tougher dermal layers of the skin.

Some monogeneans rely entirely on hooks for attachment (Figure 5), but the saucer-shaped haptors of *Entobdella* spp. (Figures 1 and 3) are attached principally by suction, generated by contraction of the musculature of the saucer or by an independent mechanism involving participation of the hooks [5].

*Leptocotyle minor*, a monogenean inhabiting the skin of the dogfish, *Scyliorhinus canicula*, has a very small haptor with no hooks. This is because the adult parasite attaches itself to the projecting region of a single scale (denticle) (Figure 6). The distal protruding portion of each denticle has no covering of skin, unlike the scales of bony fishes, and provides a hard substrate, unsuitable for the deployment of hooks. *L. minor* solves this problem by using a secretion to cement the hookless haptor to the 'naked' denticle surface [15].

As well as the posteriorly located haptor, most monogeneans are able to attach the anterior ends of their bodies to the host. Like *Leptocotyle*, this is usually achieved by deployment of an adhesive

secretion, which is employed, in conjunction with the haptor, for leech-like locomotion. *Entobdella soleae* has two adhesive pads, one on each side of the head (Figures 1 and 3A). Remarkably these pads are capable of firm adhesion even to wet, slimy, fish skin [16], but, in spite of the tenacity of the bond, the parasite is capable of detaching the pads instantly when required during locomotion.

The second anatomical feature that has been exploited by monogeneans is the fish gill [5]. Bony fishes (teleosts) usually have four gills on each side (Figure 7A). Each gill has a bony gill arch, projecting from which are two hemibranchs (or half gills). Each hemibranch comprises a row of tapering primary gill lamellae (sometimes called gill filaments) (Figures 7A and 8). Each primary lamella is flattened like a knife blade and carries two rows of closely spaced, flap-like, secondary gill lamellae, the rows projecting in opposite directions from the two flat surfaces of each primary lamella (Figures 8 and 13). The gills on each side are covered by a flap or operculum.

The secondary lamellae are the sites of gaseous exchange, for which they provide an enormous surface area. Blood flows through the secondary lamellae, giving the gills their rich red colour. Each secondary lamella consists of two thin layers of epithelium, minimising diffusion distances. Thus, unlike the relative inaccessibility of the blood supply to the skin, blood is readily accessible in the gills and is exploited by the so-called polyopisthocotylean monogeneans [17]. So close is the blood to the gill surface that there is no need for piercing mouthparts and blood-feeding monogeneans have no such equipment. Gill-dwelling monogeneans probably require little effort to rupture the thin walls of the secondary lamellae, perhaps by applying suction and/ or by application of digestive secretions. Indigestible haematin (the brown/black pigment in *Pseudaxine*, (Figure 12)) accumulates from the parasite's blood meals and is egested at intervals via the mouth.

The arrangement of the gills is such that water flows between the secondary lamellae in the opposite direction to blood flow. This counter-current system is an important adaptation for maximising gaseous exchange [5], as is also the fact that the flow of water through the gills is virtually continuous, being propelled by a buccal force pump and an opercular suction pump working in sequence. There are some differences in the arrangement of gills in an elasmobranch (Figure 7B), but, like teleosts, flap-like secondary lamellae, irrigated by a more or less continuous gill ventilating current, are the sites of gaseous exchange.

Attachment to fish gills offers a special challenge and has led to some remarkable feats of biological engineering. Surprisingly, it is the apparently delicate secondary gill lamellae that provide sites for attachment. Relatively small monogeneans, like *Amphibdelloides maccallumi* on the gills of the electric ray, *Torpedo marmorata*, insert the haptor between two adjacent secondary gill lamellae [18]. They have four large hooks, arranged in two lateral pairs (Figure 9). Each pair is capable of counter-rotation, which serves to impale the secondary gill lamellae in contact with the parasite's dorsal and ventral surfaces (Figure 9).

Blood-feeding polyopisthocotylean monogeneans are too large to fit between secondary lamellae. They have downplayed their hooks and acquired remarkable clamp-like organs which are capable of gripping one or two secondary gill lamellae (Figures 10-12) [19]. The two opposing jaws of each clamp are supported by a framework of hard sclerites (Figure 10).

Typically these blood-feeding monogeneans are symmetrical with four clamps on each side (Figure 11), but there are others that are strongly asymmetrical (Figures 12 and 13), with between 50 and 70 clamps on one side only of the body in *Axine belones* [20]. Asymmetry is related to the features of the host's gill-ventilating current. Large parasites tend to disrupt the smooth flow of water through the gill, reducing the effectiveness of gaseous exchange. Moreover, the attachment organs will be continuously under threat of dislodgement, since the water currents through the gill rarely falter. These problems are minimised by streamlining, such that the parasite interferes as little as possible with gill flow. This is achieved by attaching the clamps
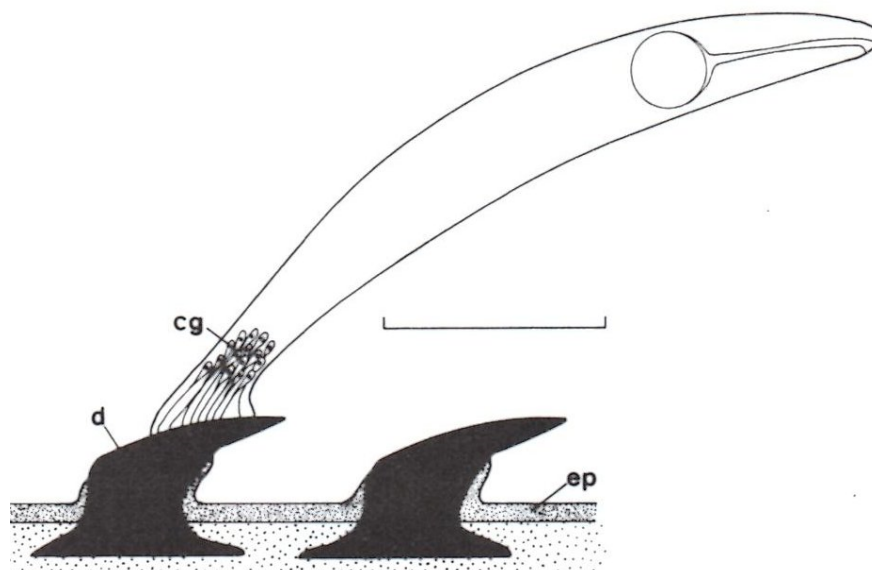


**Figure 6:** The monogenean *Leptocotyle minor* attached to a single denticle (d) of its host, the dogfish, *Scyliorhinus canicula*. cg, Cement glands; ep, epidermis. Scale bar: 0.5 mm. From Kearn [12]. Copyright © 1994, with permission from Elsevier.
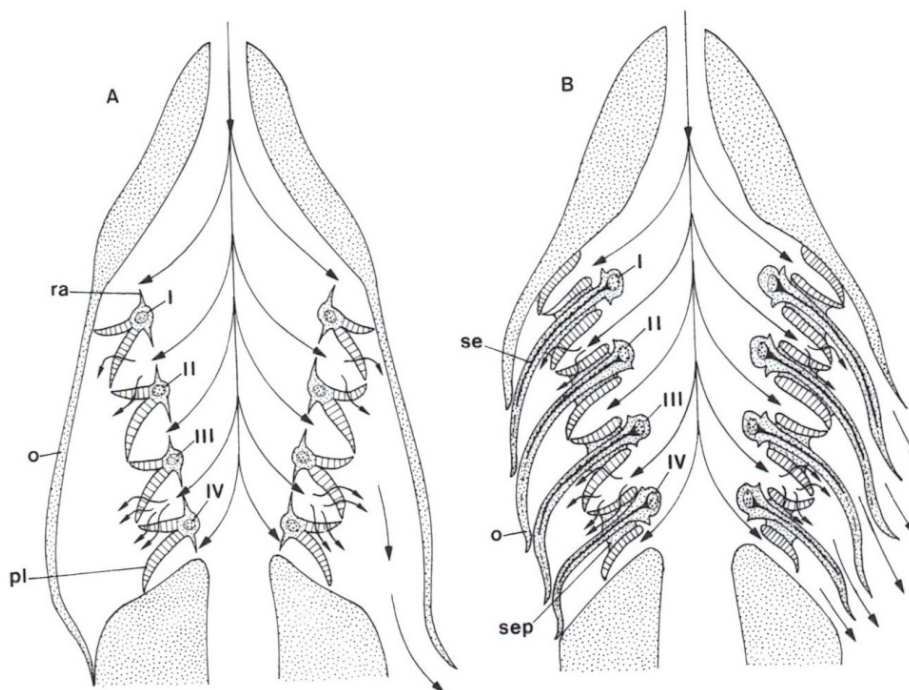
**Figure 7:** Diagrammatic sections in a horizontal plane through the buccal and gill chambers of (A) a teleost and (B) an elasmobranch showing the arrangement of the gills. The opercula are shown closed on the left and open on the right of each diagram. I - IV, gill arches; o, operculum; pl, primary gill lamella bearing secondary lamellae; ra, gill raker; se, gill septum; sep, septal canal. Large arrows indicate directions of water currents entering and leaving the gill chamber; small arrows indicate the paths of the gill-ventilating currents between the secondary gill lamellae. From Kearn [5].



**Figure 8:** Stereogram showing parts of two adjacent gill arches (ga) of a teleost. pl, Primary lamella; sl, secondary lamella. Arrows show directions of water currents. Modified from a sketch by Eleanor Skeate. From Kearn [5].

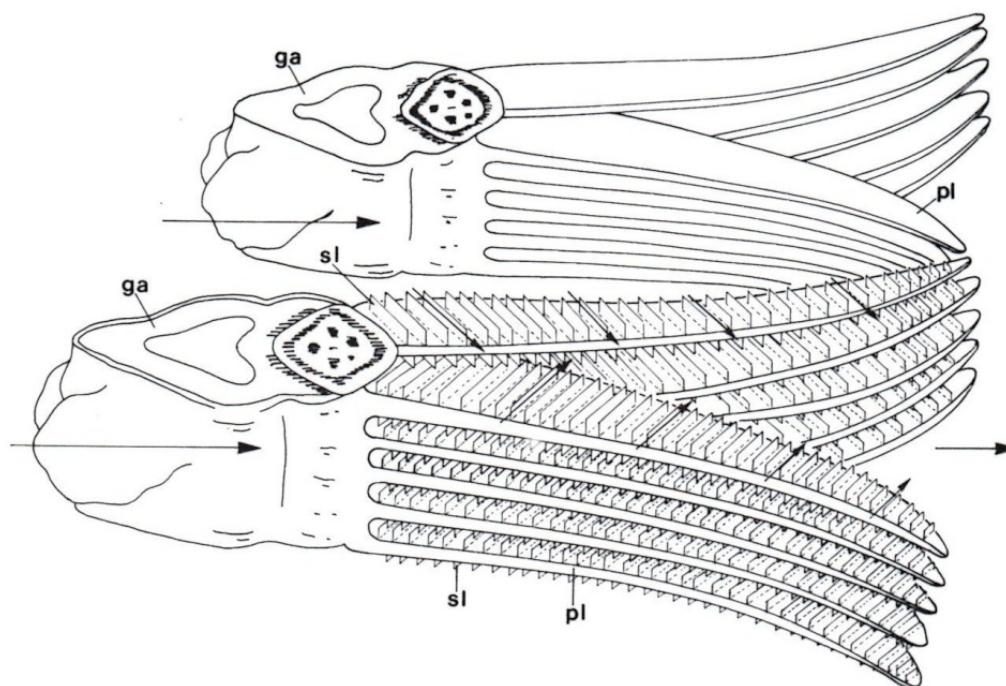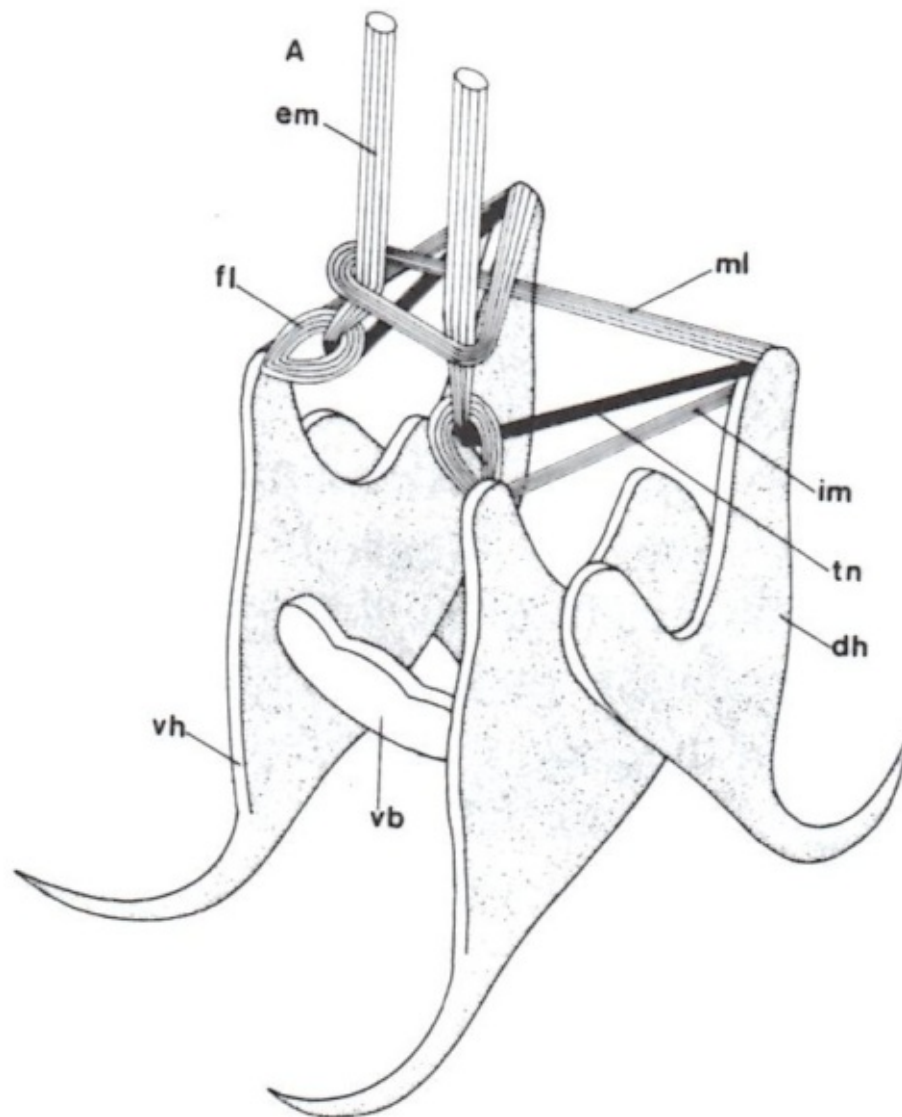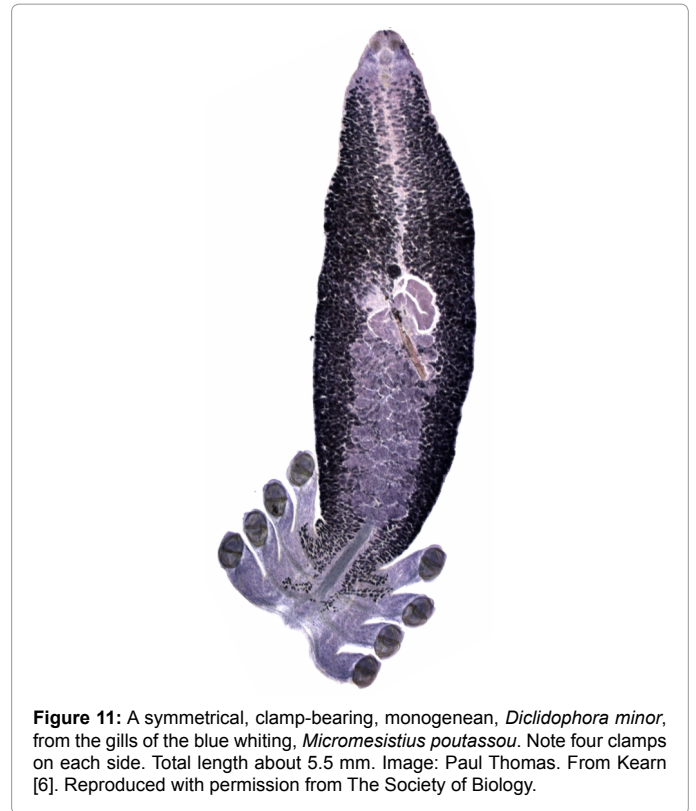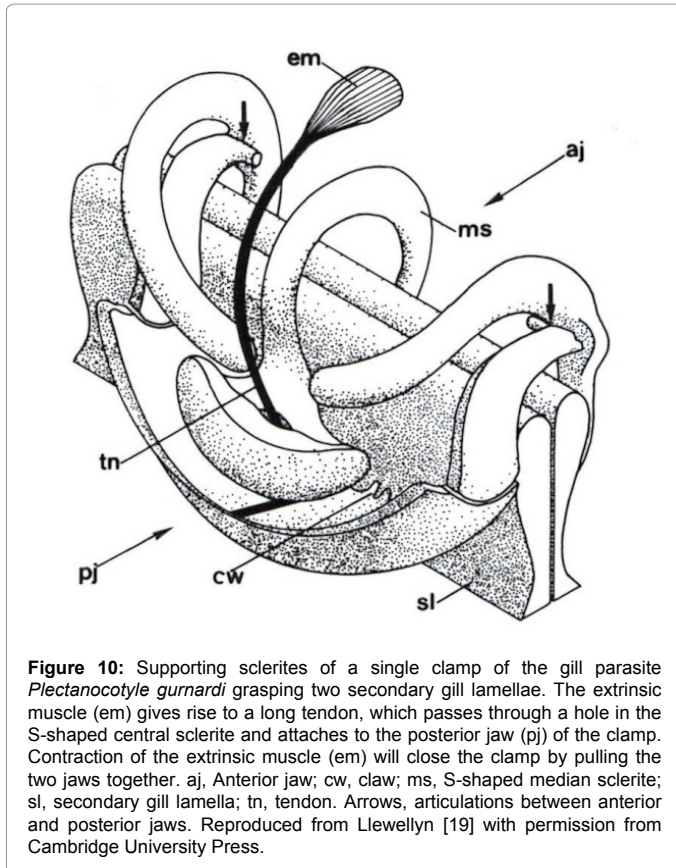**Figure 9:** Stereogram showing the principal attachment apparatus of the gill-parasitic monogenean *Amphibdelloides maccallumi*. On each side, the flat roots of one ventral hook (vh) and one dorsal hook (dh) are virtually in contact, with their hooked regions pointing respectively ventrally and dorsally. Supporting fibres are such that when the extrinsic muscles (em) and/or the intrinsic muscles (im) contract the ventral and dorsal hooks of each lateral pair counter-rotate, the hooks impaling the secondary gill lamellae in contact with the haptor's ventral and dorsal surfaces. fl, Fibrous loop; ml, muscle loop; tn, tendon; vb, ventral bar to which hooks are tethered. Reproduced from Llewellyn [18] with permission from Cambridge University Press.

upstream. Figure 13 shows the location on the gill of the asymmetrical monogenean, *Axine belones*, a parasite of the garfish, *Belone belone*. The parasite is attached to secondary lamellae on the dorsal side of a primary lamella of the outer hemibranch or half gill [20]. The clamp row is attached upstream and the shape of the rest of the body follows the course of water flow through the gill. The parasite illustrated in Figure 13 could be described as 'left-footed', but if consideration is given to a parasite attached to the opposite side (the ventral side) of the same primary lamella, this parasite would need to be 'right-footed' to be compatible with the currents flowing around it. Thus sites for attachment can accommodate either a 'left-footed' or a 'right-footed' individual and the expectation is that half the parasite population will

fall into each of these categories. Curiously most individuals of *A. belones* (87%) are 'right-footed' [20].

This begs the question of how other gill-parasitic monogeneans like *Diclidophora minor* (Figure 11) are able to retain their symmetry. This is achieved in *Diclidophora* spp. by attaching the four clamps on the left side of the body to secondary lamellae on the dorsal side of a primary lamella and the other four clamps to the secondary lamellae on the ventral side of either the same or a neighbouring primary lamella [20]. Thus all eight clamps are upstream and the body contours follow smoothly the changing direction of the gill-ventilating current.

The ciliated, free-swimming larvae of monogeneans are small and

**Figure 10:** Supporting sclerites of a single clamp of the gill parasite *Plectanocotyle gurnardi* grasping two secondary gill lamellae. The extrinsic muscle (em) gives rise to a long tendon, which passes through a hole in the S-shaped central sclerite and attaches to the posterior jaw (pj) of the clamp. Contraction of the extrinsic muscle (em) will close the clamp by pulling the two jaws together. aj, Anterior jaw; cw, claw; ms, S-shaped median sclerite; sl, secondary gill lamella; tn, tendon. Arrows, articulations between anterior and posterior jaws. Reproduced from Llewellyn [19] with permission from Cambridge University Press.



**Figure 11:** A symmetrical, clamp-bearing, monogenean, *Diclidophora minor*, from the gills of the blue whiting, *Micromesistius poutassou*. Note four clamps on each side. Total length about 5.5 mm. Image: Paul Thomas. From Kearn [6]. Reproduced with permission from The Society of Biology.



**Figure 12:** An asymmetrical, clamp-bearing, monogenean *Pseudaxine trachuri*, from the gills of the horse mackerel, *Trachurus trachurus*. Note the row of many clamps on one side only of the body and the brown or black pigment (haematin) derived from ingested host blood. Total length about 2 mm. Image: Paul Thomas. From Kearn [6]. Reproduced with permission from The Society of Biology.

it is hard to imagine how such tiny larvae are able to locate a host in the vastness of the ocean. However, the chances of larval success are improved by a variety of behavioural adaptations. Many monogeneans have rhythmical hatching patterns, larvae emerging at times when the host is more vulnerable. For example, the common sole host of *Entobdella soleae* is nocturnal and rests on the bottom during the hours of daylight. The larvae of *E. soleae* hatch soon after dawn and therefore have a stationary target host during the daylight hours [21]. On the other hand, the halibut is a large active predator and is likely to be diurnal, resting at night. This is supported by the fact that *E. hippoglossi* hatches at dusk [22].

*E. soleae* also has a second option which is not open to *E. hippoglossi*. If a sole comes to rest on or near eggs of *E. soleae* resting on the bottom, mucus from the sole stimulates hatching within a few minutes and contact with the host is likely [23]. *Acanthocotyle lobianchi* living on the skin of elasmobranch flatfishes (rays) has taken this one step further. The larvae of *A. lobianchi* have no cilia and are unable to swim. When a ray settles on eggs on the sea bottom the parasite larvae respond to urea in host mucus within seconds by rapidly lengthening the body and dislodging the lid that closes one end of the sausage-shaped egg [24]. However, the larvae have no need to swim since by elongating their bodies they can usually reach the lower skin of the resting host.

Other host-derived cues stimulate rapid hatching. The ciliated larvae of *Neoentobdella diadema*, a skin parasite of the stingray *Dasyatis pastinaca*, emerge within seconds when a shadow is cast over them by cruising or resting stingrays [25]. The ciliated larvae of *Diclidophora luscae*, a gill parasite of pouting, *Trisopterus luscus*, hatch rapidly in response to mechanical disturbance created as the hosts forage [26].
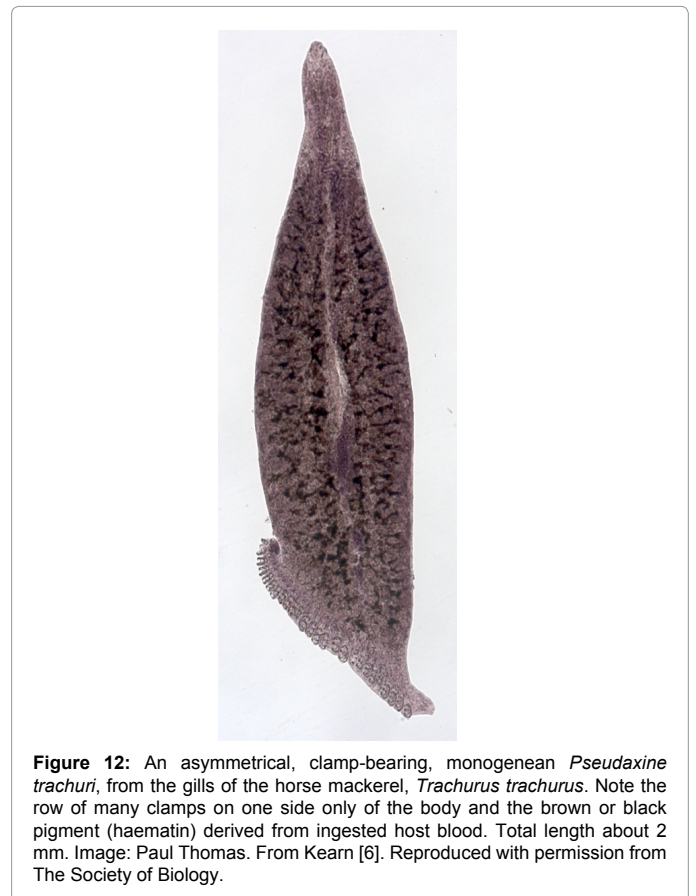
*Entobdella soleae* has another way of spreading to new hosts. Adults and juveniles can transfer when soles make contact with each other [27]. In *Neoentobdella* spp., parasitising the skin of Australian stingrays, this has gone further. Adults and/or juvenile parasites are capable of detaching themselves from the host and swimming freely, not by cilia but by undulating the body [28]. This provides an opportunity to infect new hosts without the need for hosts to make physical contact with each other.

Skin-parasitic and gill-parasitic monogeneans have no need to move about on their hosts to find food, but locomotion is important for individuals to make contact and exchange sperm. Monogeneans are hermaphrodite and are potentially capable of inseminating each other. Curiously, the clamp-bearing, blood-feeding, gill parasites appear to be sedentary, posing the question of how sperm exchange is achieved. Little is known of their reproductive biology, but some adults, for example *Diclidophora merlangi* on the whiting, *Merlangius merlangus*, tend to cluster on the gills and are close enough to mate with their neighbours [29]. The freshwater parasite *Diplozoon paradoxum*, from the gills of the roach, *Rutilus rutilus*, takes this a step further in a remarkable way. Two individual parasites fuse so that their reproductive ducts are permanently connected [5].

Readers of this article will have noticed that each of the monogeneans to which reference is made is either restricted to a single host species or to a few closely related species. For example, *Entobdella hippoglossi* has been found currently only on the halibut, *Hippoglossus hippoglossus* and *Diclidophora minor* only on blue whiting, *Micromesistius poutassou*. *Entobdella soleae* parasitises the common sole, *Solea solea*, and in addition the related sand sole, *Pegusa lascaris* and the Senegalese sole, *Solea senegalensis*. *Plectanocotyle gurnardi* has been found on the red gurnard, *Aspitrigla cuculus*, the grey gurnard, *Eutrigla gurnardus*, the tub gurnard, *Trigla lucerna* and the streaked gurnard, *Trigloporus lastoviza*, all members of the family Triglidae. This host specificity is thought to be a consequence of co-evolution - as hosts evolve and speciate their parasites speciate correspondingly, leading to a congruence between lineages of host and parasite. However, some unexpected host/parasite relationships may be the consequence of host-switching in which a parasite transfers from one host and becomes established on an unrelated host sharing the same environment. Host-switching from a teleost host is likely to explain the occurrence of gyrodactylid monogeneans of the genus *Isancistrum* on the tentacles of squid (an invertebrate) [30] and *Oculotrema hippopotami*, a polystomatid monogenean with ancestors on freshwater anurans and turtles, beneath the eyelids of the hippopotamus [31].

Each major group of fish-like vertebrates has its own distinct group of blood-feeding monogenean gill parasites [32]. The clamp-bearers parasitising the bony fishes belong to one of these groups. The implication is that early blood-feeding monogeneans may have been present on the ancestors of these fish-like vertebrates before these vertebrates diverged, possibly as far back as the Ordovician period, 440 to 490 million years ago. Thus monogeneans are very ancient - they make the dinosaurs look modern!

In spite of their hooks, suckers and clamps most monogeneans have little impact on their hosts in the wild, but some monogeneans pose a significant threat to fishes in aquaria or fish farms [33]. About
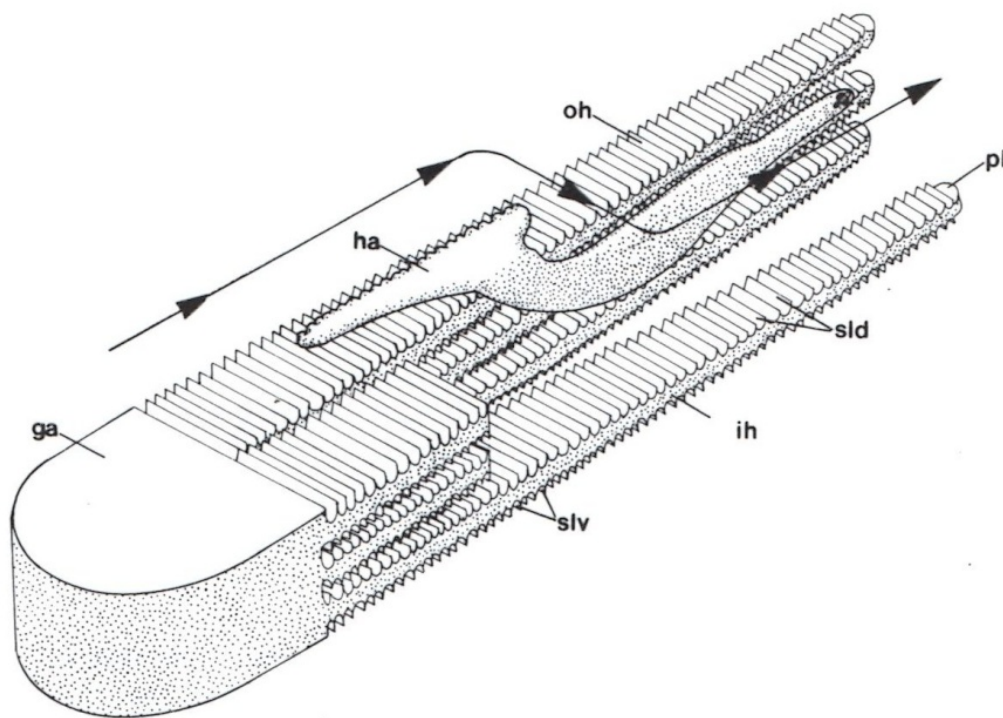


**Figure 13:** Stereogram showing the adhesive attitude of the clamp-bearing, monogenean *Axine belones* on a gill of the garfish, *Belone belone*. ga, Gill arch; ha, haptor; ih, inner hemibranch (half gill); oh, outer hemibranch (half gill); pl, primary lamella; sld, secondary lamellae on dorsal side of primary lamella; slv, secondary lamellae on ventral side of primary lamella. Arrows, direction of gill-ventilating current. Reproduced from Llewellyn [20] with permission from Cambridge University Press.

half of the soles in the North Sea host *Entobdella soleae*, each infected sole rarely carrying more than two or three relatively small adults (5 or 6 mm in length). However, in aquaria, invasion success of their larvae is much higher and populations of *E. soleae* on captive hosts increase rapidly. Eventually the epidermis may be removed faster than it is replaced by the host, the osmotic water balance may be impaired and pathogenic micro-organisms may become established, leading to death of the host.

As a consequence of viviparity the unciliated offspring of gyrodactylids may establish themselves on the same host as their parents (autoinfection), thereby avoiding the mortality to which free-swimming larvae of oviparous monogeneans are subjected. Consequently, populations of gyrodactylids on individual hosts may increase rapidly, even in the wild. Hosts may be able to limit or even eliminate this expansion by mechanisms not yet fully understood [34], but hosts unable to limit parasite numbers are unlikely to survive. *Gyrodactylus salaris* in Norway is notorious as a killer of salmon parr (*Salmo salar*), both in the wild and in fish farms. Britain is currently free of *G. salaris*.

### References

1. Müller OF (1776) Zoologiae Danicae prodromus, seu animalium Daniae et Norvegiae indigernarum characteres, nomina, et synonma imprimis popularium Havniae.

2. Van Beneden P-J (1858) Mémoires sur les Vers Intestinaux. Baillière et fils, Paris.

3. Van Beneden P-J, Hesse E (1864) Recherches sur les bdellodes (hirudinées) et les trématodes marins. Mémoires de l'Académie Royale des Sciences, des lettres et des beaux-arts de Belgique 34: 1-142.

4. Kearn GC (1998) Parasitism and the Platyhelminths. Chapman & Hall, London, UK.

5. Kearn GC (2004) Leeches, Lice and Lampreys. A Natural History of Skin and Gill Parasites of Fishes. Springer, the Netherlands.

6. Kearn GC (2011) Monogeneans, the ultimate fish parasites. Biologist 58: 28-32.

7. Bakke TA, Harris PD, Jansen PA, Hansen LP (1992) Host specificity and dispersal strategy in gyrodactylid monogeneans, with particular reference to *Gyrodactylus salaris* (Platyhelminthes, Monogenea). Dis Aquat Organ 13: 63-74.

8. Tinsley RC (1990) Host behaviour and opportunism in parasite life cycles. Parasitism and Host Behaviour, edited by Barnard CJ, Benke JM, Taylor & Francis, London, UK.

9. Tinsley RC (2013) The oncomiracidium of *Oculotrema hippopotami* Stunkard, 1924 and relationships within the Polystomatidae (Monogenea). Syst Parasitol 84: 123-135.

10. Gibson DI, Timofeeva TA, Gerasev PI (1996) A catalogue of the nominal species of the monogenean genus *Dactylogyrus* Diesing, 1850 and their host genera. Syst Parasitol 35: 3-48.

11. Bakke TA, Harris PD, Cable J (2002) Host specificity dynamics: observations on gyrodactylid monogeneans. Int J Parasitol 32: 281-308.

12. Kearn GC (1994) Evolutionary expansion of the Monogenea. Int J Parasitol 24: 1227-1271.

13. Kearn GC (1963) Feeding in some monogenean skin parasites: *Entobdella soleae* on *Solea solea* and *Acanthocotyle* sp. on *Raia clavata*. J Mar Biol Assoc UK 43: 749-766.

14. Kearn GC (1999) The survival of monogenean (platyhelminth) parasites on fish skin. Parasitology 119: S57-S88.

15. Kearn GC (1965) The biology of *Leptocotyle minor*, a skin parasite of the dogfish, *Scyliorhinus canicula*. Parasitology 55: 473-480.

16. Kearn GC, Evans-Gowing R (1998) Attachment and detachment of the anterior adhesive pads of the monogenean (platyhelminth) parasite *Entobdella soleae* from the skin of the common sole (*Solea solea*). Int J Parasitol 28: 1583-1593.

17. Llewellyn J (1954) Observations on the food and the gut pigment of the Polyopisthocotylea (Trematoda: Monogenea). Parasitology 44: 428-437.

18. Llewellyn J (1960) Amphibdellid (monogenean) parasites of electric rays (Torpedinidae). J Mar Biol Assoc UK 39: 561-589.

19. Llewellyn J (1956a) The adhesive mechanisms of monogenetic trematodes: the attachment of *Plectanocotyle gurnardi* (v. Ben. & Hesse) to the gills of *Trigla*. J Mar Biol Assoc UK 35: 507-514.

20. Llewellyn J (1956b) The host-specificity, micro-ecology, adhesive attitudes, and comparative morphology of some trematode gill parasites. J Mar Biol Assoc UK 35: 113-127.

21. Kearn GC (1973) An endogenous circadian hatching rhythm in the monogenean skin parasite *Entobdella soleae*, and its relationship to the activity rhythm of the host (*Solea solea*). Parasitology 66: 101-122.

22. Kearn GC (1974a) Nocturnal hatching in the monogenean skin parasite *Entobdella hippoglossi* from the halibut, *Hippoglossus hippoglossus*. Parasitology 68: 161-172.

23. Kearn GC (1974b) The effects of fish skin mucus on hatching in the monogenean parasite *Entobdella soleae* from the skin of the common sole, *Solea solea*. Parasitology 68: 173-188.

24. Macdonald S (1974) Host skin mucus as a hatching stimulant in *Acanthocotyle lobianchi*, a monogenean from the skin of *Raja* spp. Parasitology 68: 331-338.

25. Kearn GC (1982) Rapid hatching induced by light intensity reduction in the monogenean *Entobdella diadema*. J Parasitol 68: 171-172.

26. Whittington ID, Kearn GC (1988) Rapid hatching of mechanically-disturbed eggs of the monogenean gill parasite *Diclidophora luscae*, with observations on sedimentation of egg bundles. Int J Parasitol 18: 847-852.

27. Kearn GC (1988) The monogenean skin parasite *Entobdella soleae*: movement of adults and juveniles from host to host (*Solea solea*). Int J Parasitol 18: 313-319.

28. Whittington ID, Kearn GC (2009) Two new species of entobdelline skin parasites (Monogenea, Capsalidae) from the blotched fantail ray, *Taeniura meyeni*, in the Pacific Ocean, with comments on spermatophores and the male copulatory apparatus. Acta Parasitol 54: 12-21.

29. Macdonald S, Caley J (1975) Sexual reproduction in the monogenean *Diclidophora merlangi*: tissue penetration by sperms. Zeitschrift für Parasitenkunde 45: 323-334.

30. Llewellyn J (1984) The biology of *Isancistrum subulatae* n. sp., a monogenean parasitic on the squid, *Alloteuthis subulata*, at Plymouth. J Mar Biol Assoc UK 64: 285-302.

31. Thurston JP, Laws RM (1965) *Oculotrema hippopotami* (Trematoda: Monogenea) in Uganda. Nature 205: 1127.

32. Llewellyn J (1963) Larvae and larval development of monogeneans. Adv Parasitol 1: 287-327.

33. Whittington ID, Chisholm LA (2008) Diseases caused by Monogenea. Fish Diseases, Science Publishers, Enfield, NH, USA.

34. Bakke TA, Cable J, Harris PD (2007) The biology of gyrodactylid monogeneans: the 'Russian-doll killers'. Adv Parasitol 64: 161-376.

35. Cunningham JT (1890) A Treatise on the Common Sole. Marine Biological Association of the United Kingdom, Plymouth, UK.

36. Gusev AV (1985) Class Monogenea. Keys to Parasites of the Freshwater Fish Fauna of the USSR 2: 10-253. Parasitic Metazoa, Nauka, Leningrad. (In Russian).

37. Malmberg G (1970) The excretory systems and the marginal hooks as a basis for the systematics of *Gyrodactylus* (Trematoda, Monogenea). Archiv för Zoologi 23: 1-235.