Remarks

ON

THE BIONOMICS OF HELMINTHS.

A PAPER READ BEFORE THE SOCIETY OF TROPICAL MEDICINE AND HYGIENE.

BY

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My purpose in this paper is to advance some general considerations on the subject of helminth parasites. These will be derived from a study of the subject, not so much as it affects man, but in its wider relation to other vertebrates, and an attempt will be made to interpret in terms of general principles the facts which we know concerning human helminths. The treatment will be almost exclusively biological.

One of the first outstanding principles in helminthology is the fact that, with comparatively few exceptions, the definite or final host is a vertebrate. The exceptions are to be found amongst certain insects and myriapods which harbour adult nematodes, but no case is known of an invertebrate serving as the final host of a cestode or trematode. On the other hand, vertebrates and invertebrates alike may function as intermediate hosts. Generally speaking, therefore, invertebrates are parasitized only by larval stages, while vertebrates are subject to both larval and adult stages.

A second important fact is that helminth parasites can have no existence apart from their hosts, by which I mean that their life is indissolubly bound up in and dependent on the latter. It is true that they may survive the death of their host for a longer or shorter period, and may even make their exit from the dead host and be found at some distance from it, but their life is practically at an end, and they can never hope to make any prolonged existence thereafter. On this account it has been found impossible to keep adult helminths alive under artificial conditions for any length of time, although theoretically, if the exact physiological conditions of the habitat could be reproduced, it is not altogether an impossibility. Various larval stages have been reared in artificial media, but never beyond the point at which a living host was necessary for their continued development. In the case of intermediate stages the death of the host does not necessarily imply the death of the parasite, provided the former be eaten by some animal suitable as a final host. In such a case the parasite is enabled to complete its life-cycle; otherwise it must inevitably perish. The rare cases of heterogenesis are no exception to this, for even although in such cases a sexual cycle is passed through outside the host, the helminth eventually requires a host, and if that be withheld its life will be cut short.

Present knowledge seems to point to the fact that practically no species of animal can be considered immune to infection with helminths of one kind or another. The degree of susceptibility varies to a great extent in relation with the general habits, the mode of feeding, and certain imperfectly-known physiological idiosyncrasies. The susceptibility to the various kinds of helminths also varies in a similar way; thus the dog is particularly prone to infection with cestodes, but rarely harbours trematodes. Certain species of helminths are capable of infecting a large number of different hosts, whereas others are confined to one particular host; for example, *Taenia solium* occurs only in man, while *Fasciola hepatica* occurs in a variety of mammals. Again, some hosts harbour numerous species of helminths, even as many as ten or a dozen different species being present at the same time, while others may harbour only one species, although that may occur with great frequency and in excessive numbers.

From a medical point of view only such helminths are of interest, as a rule, as call for medical treatment, and in consequence a somewhat inaccurate idea is apt to be engendered of the true importance of helminths in general. There is a tendency to forget that cases giving

rise to symptoms form only a very small proportion of the total number actually infected. It has long been recognized that the occurrence of helminth parasites is very widespread. In 1845 Dujardin recorded that he found helminths in 53 per cent. of the 2,400 animals which he dissected, and of these, for the most part, only the alimentary canal was examined. Since that time various isolated statistics are to hand of the frequency of helminth infection amongst the different groups of animals. These are chiefly from Continental abattoirs, and are concerned with the domesticated animals. They show, however, that even in the domestic state, where a certain amount of care is exercised in the feeding arrangements, infection reaches a very high degree. At Copenhagen, for instance, Krabbe found 86 per cent. of the horses infected with *Strongylus equinus* alone, and practically 100 per cent. harboured helminths of some kind or other. He also found that 67 per cent. of dogs had intestinal parasites. This figure would undoubtedly have been much larger had the other viscera been examined in addition. Cartice, in 1887, found 87 per cent. of sheep in Colorado infected with the tapeworm, *Moniezia expansa*. Hertwig, in 1890, at the Berlin abattoir, examined 150,000 adult bovines, and met with *Fasciola hepatica* in 75 to 80 per cent. These figures form rather a disagreeable commentary on the cleanliness with which our domestic animals are housed and fed. In birds Hausmann has recorded an infection, with trematodes alone, of 30 per cent., and Wolffhügel 21 per cent. These were mostly inland birds, but in aquatic birds the percentage is much higher. On the east coast of Britain, for instance, I have found infection in over 90 per cent. In reptiles and amphibians I have no figures at hand, but here also infection is very high. Finally, in fishes I have found a constant infection of over 80 per cent. in the British fishes. In view of these figures, then, it cannot be regarded as an excessive estimate that 75 per cent. of all vertebrate animals are infected with helminth parasites of some kind or other. This may serve to indicate in a crude way the extent to which helminth parasitism enters into the economy of Nature.

Such being the case, we can hardly fail to come to the conclusion that the presence of helminth parasites in vertebrate animals must be regarded not as an abnormality, but as a normal condition, just in the same way as the presence of intestinal bacteria may be considered normal. The belief has more than once been advanced that helminths may even exercise a beneficial influence on their host. To some this idea may appear quite in discord with the medical conception of parasite as something loathsome and highly dangerous. The belief is founded on the fact that most helminths secrete a more or less irritating substance which may have the effect of stimulating digestion. There is, however, no direct evidence of this, but it is now generally agreed that the influence of helminths for the most part is, if not beneficial, at least comparatively innocuous. It is only when some vital organ is invaded, or when infection reaches an excessively high degree that harm results. In the latter case, however, it is difficult to know where to fix the limit. For instance, Dujardin quotes two cases, in one of which a black stork harboured 24 specimens of *Filaria labiata* in the lungs, 16 *Syngamus trachealis* in the trachea, more than 100 *Spiroptera alata* in the wall of the stomach, several hundred *Holostomum excavatum* and an *Echinostomum revolutum* in the small intestine, 100 *Chaunocephalus ferox* in the large intestine, and 22 *Cathaemasia hians* in the oesophagus, without showing any signs of distress. The other was a two-year-old horse, in which were found 500 *Ascaris megalocephala*, 200 *Oxyuris curvula*, 200 *Strongylus equinus*, several thousand *Strongylus tetracanthus*, 70 *Anoplocephala perfoliata*, 300 *Filaria papillosa*, and 6 *Cysticercus fistularis*. It is not at all uncommon to find several thousand parasites in one host, and one meets occasional references to the removal of a "bucketful" of tapeworms or ascarids from an animal which had previously shown no signs of inconvenience. It has been maintained by some that it is only when the general health of the host is impaired by some other cause that intestinal parasites begin to have an injurious influence. This, however, stands in need of confirmation.

If this condition of affairs, then, can exist in domesticated animals which are under constant observation, we

need not be surprised to find a similar condition amongst animals in a wild state. The rarity with which the latter appear to actually suffer from, or be incapacitated by, the invasions of helminth parasites is most striking. I cannot recall more than half a dozen instances in over a thousand birds and fishes.

In this connexion, however, three points must be borne in mind: (1) It is difficult for us to determine when an animal is suffering from illness, unless in pronounced cases; (2) the chance of such diseased animals surviving the struggle for existence and being brought to us for examination is small; (3) there is the possibility of immunity enabling the host to withstand the ill effects liable to be produced by parasites. With regard to the first point, veterinary surgeons are able to detect illness in such animals as horses and cattle with comparative readiness, and yet even they frequently report cases of extensive helminthiasis without apparent symptoms. The second point need hardly be commented upon, for it is only too well known that in Nature an animal that is seriously incapacitated very soon drops out.

The tolerance towards extensive helminth infection has more than once been ascribed to immunity, according to which antibodies are elaborated by the host to counteract the effects liable to be produced by any particular parasite. It has been found that many helminths secrete or possess within themselves a specific toxin, capable of producing ill effects under certain circumstances. The nature of these toxins, however, and the exact manner of their action, are matters on which we have as yet little definite knowledge. It is known, for instance, that *Dibothriocephalus latus* contains three different substances—namely, a haemolysin, a haemagglutinin, and a proteolytic ferment, each of which may produce evil consequences on its host, but under what circumstances exactly is still a matter of doubt. Why only certain cases suffer from the presence of this parasite is difficult to understand. That the illness is not the result of a massive infection, as in ankylostomiasis, seems abundantly proved. The anomaly has been explained on the ground that the toxins are only liberated on the death of the parasite, and that they produce their ill effects only so long as the dead parasite is retained within the host. This theory has also been advanced in the case of hepatic fascioliasis, but it lacks confirmation and does not appear to agree with other facts.

A large proportion of such pathological lesions as do occur are due to larval forms. The numerous cestode cysts of mammals, and the cestode and nematode cysts in the body cavity of fishes, may be instanced in vertebrates, while in invertebrates larval cysts of all kinds abound, frequently leading to serious lesions. Here, again, it is wonderful to what an extent helminth infection can go without causing much apparent distress to the host. Forty years ago McIntosh observed that the common green crabs (*Carcinus moenas*), at St. Andrews, were extraordinarily subject to infection with larval trematodes. He found their bodies simply riddled with the minute globular cysts which pervaded every organ and tissue, the liver, gonads, muscles and nerves being especially infected. I have recently confirmed McIntosh's observations, not only at St. Andrews, but in other parts of the country. This infection is not confined to isolated individuals, but occurs in practically all to a greater or less degree. Occasionally the infection is so enormous that nearly one-half of the crab's anatomy is replaced by trematodes. The edible crab (*Cancer pagurus*) is a victim to the same infection, but to a considerably less extent.

It seems but natural that larval forms should cause more inconvenience to their hosts, for it is to their advantage that the latter should be weakened and thus more readily fall a prey to an animal which will serve as a final host. On the other hand, the adult parasite has nothing to gain by causing the death of its host. By doing so it terminates its own existence and lessens the chance of dissemination of its offspring.

The study of tropical diseases shows us that, in an uncivilized or semicivilized state, man is much more subject to infection with helminths than under civilized conditions. The widespread prevalence of such parasites as *Ankylostoma duodenale* and *Schistosomum haematobium*, and the relatively small proportion of cases in which

serious illness is the result of their presence, are indications that man, under such circumstances, approaches very closely to the condition I have described above as occurring in other animals. It is well known that individuals can get along fairly comfortably although heavily infected with helminth parasites, but it is just as well known that a certain limit is eventually reached, resulting in serious illness or death. It is obvious that parasitic infection is associated with living in a primitive state. Modern civilized cleanliness and sanitary arrangements have altered matters to a considerable extent and have rid man's body of what might be regarded as his natural heritage of parasites. At the same time, however, that they have made him less accustomed to parasitic guests, they have rendered him more intolerant of their evil influence when they do effect an entrance.

The typical life histories of helminth parasites are so familiar that I need only refer to them in brief. Nematodes, generally speaking, have by far the simplest life-history, and in many cases are almost entirely without metagenesis. The simplest cases are provided by *Oxyuris*, and many ascariids in which the ova extruded from one host are swallowed by another or the same host. In *Oxyuris* the ova immediately they appear in the faeces are in a condition to reinfect. Some ova require to remain under external conditions a longer time before they are ready to produce adults again. A step further is evidenced by those forms in which the larva is liberated from the ovum, and is only suited for reinfection after it has lived a certain period as such. *Ankylostoma duodenale* appears to be of this class, although its life-history is complicated by the fact that before it can reinfect it must assume a sort of free encapsulated state, by forming a sheath around itself. In the next type we have the embryo entering some intermediate host and becoming encysted there. This is by far the commonest life-cycle, and is found in a large number of nematodes and most cestodes and trematodes. A more complicated history is shown by some nematodes which pass through a second sexual stage outside the body. The larvae from this second stage reinfect the host. The remarkable life-histories of the filariae and *Trichinella spiralis* may be mentioned here. No part of the cycle takes place under external conditions, but the larvae pass the corresponding stage of their career in the blood. The conditions, however, are to some extent analogous, for blood is an aerobic medium, and, according to some observers, the presence of oxygen is necessary for the development of larvae. The complications which are introduced in the case of cestodes are not numerous, and usually consist of a multiplication by budding of the larva within the intermediate host. In the case of trematodes, however, much more elaborate histories may be evolved, and more than one intermediate host may enter into the cycle. There are four larval stages through which a trematode passes, namely, the miracidium, sporocyst, redia, and cercaria. The first stage is invariably spent in water. Each of the other three, however, may be passed through in a different host. The miracidium may enter one host and give rise to the sporocyst. The latter, by a process of internal budding, produces rediae, which may be set free and enter a second host. In this it again, by a process of budding, gives rise to cercariae, which may in their turn be set free and infect a third host, which is eventually eaten by the final host. All kinds of modification, however, may enter. Thus the sporocyst may take time by the forelock, and produce cercariae instead of rediae, and this happens fairly frequently. Again, it may take a step in the other direction, and produce a second brood of sporocysts, and the rediae also may reproduce rediae instead of cercariae. Occasionally, instead of wandering from one host to another, it passes the whole three stages in one host, or two in one host and one in another. Sometimes the process is very much reduced, the sporocyst producing cercariae, which never make their escape until they find themselves in the alimentary canal of their final host. There may be cases in which intermediate hosts are entirely absent, the miracidium simply effecting an entrance into its final host and becoming adult there. This seems to be the case with *Schistosomum*, in which, hitherto, efforts to discover an intermediate host have been unavailing. The intermediate hosts of nematodes, when present, are usually fishes or insects, occasionally crustaceans; cestodes seem to like

worms and molluscs as well as fishes, while trematodes show a great preference for molluscs.

The life-histories of most human helminths have been worked out to a more or less satisfactory extent. Owing, however, to the difficulty of discovering intermediate hosts, several remain doubtful. In the case of domesticated animals a considerable amount of work has also been done, with successful results. With regard to the rest of the animal world our knowledge is very meagre. A large number of adult helminths are known, with no corresponding larval stages, and vice versa. This to some extent is the result of imperfect description. A further difficulty is that of distinguishing larval forms from one another, possessing as they do so few specific features. For the most part, all that can be done in elucidating life-histories is to compare descriptions of adult forms with those of larvae and hypothecate their connexion if other conditions point to its being a natural or likely one. Feeding experiments are exceedingly difficult to carry out in the case of birds and fishes.

The paths of infection are two, the mouth and the skin, and of these the former is by far the commoner. Depending on the life-history of the parasite, introduction by the mouth may take place in water, in food, on dirty fingers, and rarely, if ever, by the air. Introduction through the skin is effected either by the active efforts of the larvae when the hands or feet are exposed in water or damp places, or through the agency of biting insects.

It is practically an undisputed fact that no helminth parasite is capable of multiplying sexually within the body of its host. It is an essential condition that the ova or larvae should pass out of the body of the host before they can proceed to grow again. This is generally considered to be due to the fact that the larvae require aerobic conditions for their development. This may well be the case, but the simplest explanation is found in the well-known developmental doctrine that "ontogeny is an abbreviated recapitulation of phylogeny," or, in other words, that the life-history and development of an individual tends to be a more or less perfect summary of its ancestral history.

The introduction of intermediate hosts is a difficulty for which various explanations might be advanced. It is generally agreed that trematodes and cestodes are derived from the Turbellaria, or rather that they have a common ancestry (although Ssinitzin has recently advanced the somewhat extraordinary opinion that the digenetic trematodes have an ancestry in common with the lower crustacea); in the same way the parasitic nematodes are derived from the free-living nematodes. Many of the Turbellaria and free-living nematodes show a tendency towards parasitism, and in fact a large number of the latter are parasitic in the larval stage. It may be considered that prior to the advent of the vertebrates many of the helminths had already become parasitic in invertebrates. With the advance in the evolution of the vertebrates the invertebrates naturally became their chief source of food supply, and it would frequently happen that an invertebrate harbouring a helminth would be ingested by a vertebrate. By some means, which it would be vain to attempt to explain, except possibly by mutation, the helminth became adapted for living in the intestine of the vertebrate. Here it would produce young, which, however, not being trained to parasitism, would find their way back to external media. Growing older, the tendency towards parasitism would again become strong, and they would seek a convenient invertebrate. Thereupon the cycle would be repeated, and we may suppose that the tendency to become adult in invertebrates gradually disappeared, until the present state of affairs was reached, in which the helminth proceeds only a certain distance towards maturity in the invertebrate. Semi-parasitic nematodes, such as *Gordius* and *Mermis*, show that a somewhat reverse process may have taken place in so far as it was the young of these species which took shelter in invertebrates, and getting older and more able to look after themselves, they returned to a free life. We may suppose that some of these protected larvae when swallowed with their host by a vertebrate found conditions very much to their liking, and became sexually mature in the new environment. Such problems as these, however, are purely speculative.

In introducing the subject of the specificity of helminths

with regard both to host and habitat, I wish it to be distinctly understood that it is not my intention to dogmatize on the matter; I intend simply to lay before you the general principles which to me seem to regulate the distribution of helminths in their various hosts and habitats. It would be vain to endeavour to formulate hard and fast laws, admitting of no exceptions, for such laws are entirely unknown in Nature. It must be remembered that Nature is in a state of continued flux, and that the phenomena to be observed at any particular instant comprise two components: on the one hand, those which are in a state of relative stability or equilibrium for the time being, and on the other those which are in a state of progression or retrogression. It must also be remembered that evolution has not advanced at the same rate in every direction; along some lines it has apparently remained stationary for very lengthy periods. Thus the present biological picture presents organisms on which evolution has acted to a very high degree, and at the same time others, almost archetypic, in which the process has been arrested for many ages. Helminths are in no way exempt from the same conditions, and this must be borne in mind in dealing with the matter in hand.

The idea of specificity is no new one. Even in the beginning of last century we find that helminthologists attached a certain weight to it. This is most evident in the case of Dujardin, who treated helminthology more from its bionomic than from its systematic aspect. Later, however, the principle was hardly tenable, for species, apparently similar, were found in all manner of different hosts and habitats. Such species, however, were only superficially similar, and the inability to distinguish them was due entirely to the failure of methods of differentiation. In certain instances there has been a tendency to carry the principle of specificity to an extreme degree, each parasite being regarded as specific for a particular host. This view is quite as unjustifiable as the complete denial of any specificity. My intention here is to show that the degree of specificity is an intermediate one, that no hard and fast rule underlies it, and that it shows the same amount of variation, with the same anomalies and exceptions, as is to be met with in other biological phenomena. It will be shown that the specificity is not so much between one species and another—although that occurs frequently—as between one genus and another, or between two subfamilies or two families. Further, the hosts of these species and groups may be isolated species of vertebrates, or genera or groups.

It will be necessary first of all to refer briefly to the classification of the helminths. As in many other branches of biology the taxonomy is in a rather incomplete state. It is only within the last dozen years that anything approaching a natural classification has been attained. The reason for the slow advance is not far to seek. Throughout the animal kingdom the systematic differentiation of one species from another is based to a large extent upon the study of external characters, such as the number, arrangement and shape of appendages, and this is found to be quite a satisfactory working method in the majority of cases. With the helminths, however, it proved miserably inadequate, nor is that surprising when one considers the structure of a tapeworm or distome. The external features are few and capable of little permutation. The dimensions, shape and colour of the body, the situation and relative sizes of the suckers, the presence of spines, papillae, or other simple appendages, and the position of the genital aperture sum up all there is to work upon. The absolute insufficiency of these means of diagnosis is apparent when we find that until comparatively recently a large majority of all tapeworms were included in the genus *Taenia*, and the greater half of trematodes in the genus *Distomum*. As a result, twenty years ago the genus *Taenia* comprised nearly 500 species, and the genus *Distomum* well on to 1,000, probably two of the largest genera that have ever existed in zoological nomenclature. The descriptions of older writers are in many cases practically useless, as they could apply equally well to half a dozen different species. Attempts were repeatedly made to deal with these cumbersome groups, but as they were all based on external features they were, almost without exception, unsuccessful. It was not until a study of internal structures disclosed their wonderful variety that systematic and natural classifi-

cation became possible, and we owe the material advances that have since been made, in a large measure to Professor L. 1033, of Cairo. The method has led to the differentiation of innumerable allied species, and it would be no exaggeration to say that the number of known species of helminths has been doubled within the last ten years. The erstwhile genera *Taenia* and *Distomum* have been subdivided again and again until they have come to represent taxonomic units of higher rank even than families. These innovations have not materially affected the broad lines of classification, although they have influenced their relative value. The point which I wish to emphasize, however, is that in place of the former apparently homogeneous genera *Taenia* and *Distomum*, we have now a number of distinct groups each with its respective characteristics, but all more or less intimately and naturally related. It is with these groups and these subdivisions that I shall deal, for the taenias and the distomes, together with the nematodes form by far the largest proportion of helminths. It will be impossible in the time at my disposal to deal with each of these three classes, so that I shall content myself for the most part with the treatment of the distomes. The remarkable diversity of their structure and habitat, moreover, makes them most suitable for illustration of the principle I wish to lay before you.

From the point of view of habitat the alimentary canal cannot be regarded as one homogeneous whole, for apart from the mouth, oesophagus and stomach, each of which presents distinct conditions, the intestine shows at least four separate habitats corresponding to the anatomical and physiological divisions. It is well known that *Ankylostoma duodenale* occurs almost invariably in the jejunum, *Ascaris lumbricoides* in the ileum, *Trichuris trichiurus* in the caecum and *Oxyuris vermicularis* in the colon and rectum. These are four distinct types of nematodes, and it might reasonably be imagined that we had here a high degree of specialization in an extremely highly organized host. That, of course, is true, but the principle is the same throughout. In birds, for instance, it is not uncommon to find four different species of distomes in the intestine at one time, each maintaining a distinct and circumscribed area. In fishes the same holds good. Cases, however, not uncommonly do occur where there is a certain amount of intermingling of different species, but these are usually closely related species.

Practically every organ and tissue in the body may be the habitat of helminths, but, excluding larval forms, we find the most frequent habitats are the alimentary canal, the liver and gall bladder, the respiratory passages and lungs, or gills in the case of fishes, the urinary system, the vascular system, and the subcutaneous tissue. In the case of birds the eyes and the bursa Fabricii, an appendix of the cloaca, are not uncommon seats of infection; the swim bladder is an additional seat in the case of fishes. Generally speaking, then, the only organs that escape are the brain, the muscles, and the genital system. The brain and muscles are obviously not suitable for the life of adult helminths, but it is curious that the genital passages should escape in the way they seem to do. A few cases are on record of adult helminths being found in the reproductive organs, but they were almost invariably errant forms that had strayed from the intestine. *Oxyuris vermicularis* has even been found in the pouch of Douglas, having wandered there presumably via the uterus and Fallopian tubes. An interesting occurrence, of which several records exist, is the inclusion of a trematode, *Prosthogonimus pellucidus* (V. Linstow) within the white of a hen's egg. The explanation is simple. The species lives in the bursa Fabricii, and occasionally wanders into the rectum and uterus. In the latter it becomes entangled in the albumen before the shell has been formed.

Each habitat is suitable for one or more species of helminth, and it may be taken as a general rule, which, however, must not be applied with too unrelaxing strictness, that nearly-related species tend to inhabit the same situations in their various hosts. Thus, in mammals the *Fasciolidae*, of which *Fasciola hepatica* is the type, all inhabit the liver and gall bladder, although the genus *Fasciolopsis* is an exception. *Fasciolopsis*, however, appears to live high up in the intestine in close proximity

to the bile duct, and may be regarded as a transition stage between an intestinal and a hepatic parasite. *Fasciolella* may come in the same category. The liver-frequenting habit of the *Fasciolidae* is found not only in terrestrial mammals but in marine mammals as well, for in the porpoise we find the *Brachycladiinae*, a subfamily of the *Fasciolidae*, infesting the liver and causing liver-rot, exactly similar to that in sheep. We find representatives of the same subfamily, namely, *Lecithodesmus goliath* (V. Ben), and *Orthosplanchnus arcticus* Odhner, and *O. fraterculus* Odhner in whales and seals. Another group of mammalian hepatic distomes is the *Opisthorcinae*. This is a subfamily nearly related to, but not included under, the *Fasciolidae*. In man we are familiar with *Opisthorchis novaezebrae* Braun, *O. felineus* (Rivolta), *Clonorchis sinensis* (Cobbold), and *C. endemicus* Looss. *O. felineus* occurs in several other carnivorous mammals; *O. tenuicollis* (Rud), a very closely related species in the seals, and *O. lancea* (Dies.) in the dolphin. Some species of *Opisthorchis* are found in the liver of birds, as, for instance, *O. longissimus* (V. Linst.) in *Ardea stellaris*, *O. simulans* Looss, and *O. geminus* Looss, in several birds. A closely allied genus, *Metorchis*, includes two liver parasites of the cat, *M. albidus* (Brn.), and *M. truncatus* (Rud). These also occur in the grey seal (*Halichoerus grypus*). Here again some representatives of this genus are found in the liver of birds, for example, *M. crassiusculus* (Rud) in the buzzard, (*Buteo buteo*), and *M. xanthosomus* (Crepl) in the lesser grebe (*Podiceps minor*). A distantly related subfamily, the *Telorchinae*, occurs in the liver, or in one case the duodenum of reptiles. The third great class of liver flukes, properly so called, is the subfamily *Dicrocoeliinae*, but this is almost exclusively a class of bird-trematodes. The only mammalian representative is *Dicrocoelium dendriticum* (Rud) (= *D. lanceatum* St. and H.), but this species is quite as widespread as *Fasciola hepatica*. Numerous species of this and the two allied genera *Lyperosomum* and *Athesmia* occur in the liver and gall-bladder of birds. Amphibia are practically free from liver helminths. Fish also rarely harbour adult parasites in the liver or gall-bladder. Amongst the few cases may be mentioned *Fellodistomum fellis* (Olsson), and *F. agnotum* Nicoll in the cat-fish (*Anarrhichas lupus*), and *Anisocoelium capitellatum* (Rud), in *Uranoscopus scaber*, but these forms are very different from any of the mammalian liver flukes. In the *Fellodistominae* we have another example of two genera, one of which, *Leioderma*, lives in the intestine close to the opening of the bile duct, and the other is a purely gall-bladder parasite.

Owing to the enormous number of exclusively intestinal helminths it will be impossible to refer even briefly to them in this connexion, so that I shall pass on to the other parts of the alimentary canal. Distomes rarely inhabit the stomach or oesophagus in mammals or birds, but in fishes there is a large family, the *Hemiuridae*, the members of which live almost exclusively in the stomach. Again in birds the genus *Clinostomum* contains a large number of species, all of which live in the oral cavity; the several species of the genus *Haliptegus* exclusively in the mouth of frogs. The cloaca, too, in birds with its appendix the bursa Fabricii, harbours numerous distomes, which fall into two or three more or less well-defined groups. In the lungs we find another favourite seat of trematodes. In man there is the common *Paragonimus westermanni* (Kerbert), which shows several features of resemblance to *Fasciola hepatica*. It also occurs in several carnivores. In addition there is *Paragonimus rudis* (Dies.) from the otter (*Lutra brasiliensis*) and *Paragonimus compactus* (Cobbold) from the mongoose (*Mungos fasciatus*). No distomes have ever been described from the lungs of birds, although a few have occasionally been met with in the trachea. Lung parasites of any kind, in fact, are very uncommon in birds, but I cannot venture to offer any explanation of this rather curious circumstance. In amphibia, on the other hand, the lungs are a favourite seat for parasites of all kinds, and we find here a special subfamily, the *Haplometrininae* Pratt, the chief genus of which is *Pneumonoeces* Looss. The members of this group are found only in the lungs of amphibia and a few reptiles (genus *Macrodera*). In fishes we have an entirely different state of affairs. External gills take the place of internal lungs, and here we find a distinct class of trematodes, which are radically

different from the distomes both in structure and in development. Their life-history is direct, with no intermediate host. They belong to the order *Monogenea*, and are generally referred to as *Ectotrematodes*. There are numerous genera and species, with much diversity of structure, but as they do not concern us here we shall not discuss them further.

The next viscus we may consider is the bladder and urinary organs. Here, again, we find distinct groups, constantly inhabiting this system and no other. Urinary parasites are comparatively infrequent in mammals and birds, the only common ones being the nematodes, *Eustrongylus gigas* and various species of *Trichosoma*. In reptiles, amphibians and fishes, however, we have a large homogeneous family of trematodes, the *Gorgoderidae*, which includes the genera *Phyllodistomum* from fishes, *Gorgodera* and *Gorgoderina* from amphibians, and *Plesiochorus* from reptiles. The last illustration which I shall take in this connexion is the case of the vascular system. Here we have the well-known *Schistosomum haematobium* and *S. japonicum*. These do not belong to the class *Fasciolidae*, but represent a small separate class, the *Schistosomidae*. A species, the same as or closely resembling *Schistosomum haematobium*, occurs in some of the primates. Other two species, *S. crassum* and *S. indicum*, are found in the ox and sheep. The most closely allied genus is *Bilharziella*, which comprises several species parasitic in birds; and a third recently described genus, *Gigantobilharzia*, is also found in birds. These are all the blood trematodes so far as known.

From a consideration of the foregoing, the general application of the principle of specificity of habitat can hardly fail to be clear, and, to my mind, there could be no better demonstration of the validity and correctness of Looss's system of classification. It is an axiomatic biological principle that related species and genera have common habits. Thus, all the carnivores are flesh-eating, wild, fierce animals, lithe of body and swift of foot, and, generally speaking, have habits very much in common. Subdividing them further into *Felidae*, *Canidae*, and *Ursidae*, we find constant differences in habit between the groups, which correspond to their morphological differences. The illustration of this correlation between habit and structure could be carried to the various genera. It is thus not surprising that the same has been found to hold good among the helminths. Moreover, we have several interesting examples of the phylogenetic transmission of acquired habits. Thus, amongst the *Fasciolidae*, the *Brachycladiinae* may be presumed to have begun to diverge from the parent fasciolid stock at the time when the cetacea first took to an aquatic life, but the hepatic habit remained impressed upon them, so that they continued to be liver parasites.

Turning for a short time to what is, in a sense, the converse of the foregoing, but at the same time an amplification of it: it has been shown that there is a specificity of organic habitat, it will now be shown that there is a specificity of host, always allowing for a certain number of exceptions, as in the first case. This principle is well known to those who have had to work experimentally with helminths. The most familiar case is that of *Ankylostoma duodenale*, which several workers have repeatedly endeavoured to introduce into animals other than man, but with very rare success. Dogs have occasionally been infected, but it has been found impossible to do the same with rabbits, guinea-pigs, etc. Again, it is impossible to infect the dog with *Taenia solium*. These, however, are but instances of a very general rule, of which I shall proceed to give a few more comprehensive examples. Of the true liver flukes, the *Fasciolidae* are strictly confined to mammals, the *Opisthorchiinae* are found equally in mammals and birds, the *Dicrocoeliinae*, with one exception, exclusively in birds, and the *Telorchiniinae* entirely in reptiles. No representatives of these are found in any of the lower vertebrates. Subdividing the *Fasciolidae*, the *Fasciolinae* are, with a few doubtful exceptions, restricted to the primates, ruminants, and, possibly, marsupials; and the *Brachycladiinae* to the cetacea and pinnipeds. With the *Fasciolinae* it is impossible to reduce the specificity to greater detail; but in the *Brachycladiinae* we have the genus *Brachycladium* con-

fined to the cetacea, *Lecithodesmus* to the whales, and *Orthosplanchnus* to the seals.

The Cyclophyllid or Taenioid cestodes form another group, which is confined, with only three exceptions, to the mammals and birds. In this group sixty-five genera have already been distinguished. One of these is amphibian, another reptilian, and a third has mammalian and reptilian representatives. Of the other sixty-two, forty-two are exclusively confined to birds, and eight to mammals, while twelve are common to both. There is thus evidently a preponderating partiality towards birds.

There are nine families, of which three are exclusively avian. The three largest families are the *Anoplocephalidae*, the *Davaineidae*, and the *Hymenolepididae*. The first is typically mammalian, the other two typically avian. The *Anoplocephalidae* contain six of the eight exclusive mammalian genera. The four other genera contain a few avian forms. In the *Davaineidae* only one (*Davainea*) of the six genera contains mammalian forms, and these are isolated cases. In the *Hymenolepididae* twenty-three genera are exclusively avian, two mammalian, and five contain representatives of both, but, except for *Hymenolepis*, the mammalian forms are few. This differential process could be carried to the individual species, but it will be hardly necessary to enter into such detail. It will be sufficiently clear, from the facts I have already put forward, that a remarkable degree of specificity does exist, but that there are certain meeting-places where the various genera and species become less specific. This is particularly evident in the case of large and flourishing genera, such as *Hymenolepis*, which, as a type, has apparently become adapted—partly by the nature of its life-history, partly by its own physiological requirements—to varying conditions in a large number of different hosts. As a genus, however, it is not very homogeneous, in spite of the remarkable uniformity of its fundamental structure.

A knowledge of the general facts of helminthology is essential to the study of the particular forms which parasitize man, just as much as a general knowledge of protozoology is essential to the study of malaria and allied diseases. It is evident that the occurrence of helminth parasites in man is only an instance of a general phenomenon in nature. We have seen that no animal is exempt from the attacks of helminths of some description or other, and that the less civilized races of mankind are practically in the same condition. We in this country owe our comparative freedom from helminths to the amenities of civilization, but when these fail this exemption disappears. From the point of view of helminthology, then, civilization may be regarded as consisting of three factors—namely, the cooking of food, the wearing of clothes, and the application of sanitation and personal cleanliness. These are the three chief means of defence against helminths. We saw that food was the essential factor in the transmission of parasites in the vast majority of cases. Infection with trematodes and cestodes (which are heteroxenous) can be acquired only in this way, with the doubtful exception of schistosomiasis. This, however, applies only to a limited extent in the case of nematodes (which are monoxenous). The most effectual remedies against the inroad of platyhelminths are proper cooking of food and filtration of drinking water. All parasites are killed by exposure to a temperature of 100° C. (or even less), but it is of importance that the whole of the food be raised to this temperature, not merely the exterior. Most natural waters contain minute crustaceans and other animals, which frequently harbour helminth larvae. Careful filtering, however, entirely removes those. The wearing of clothes is not of the same far-reaching importance, but it appears to be essential in the case of *Ankylostoma*, *Pinaria*, and *Schistosomum*. Sanitation and cleanliness are of little less importance than the proper cooking of food. They are specially important from an epidemiological point of view. The only means of dealing with an epidemic consists in the immediate destruction or disposal of the faeces from the infected cases, and in scrupulous personal cleanliness amongst those exposed to infection. Were these measures strictly carried out, there would be no such outbreaks of ankylostomiasis as have been notorious in Europe of recent years. It is this third factor which is most largely concerned in the

spread of nematodes. There remains a fourth factor, which is not so directly connected with, or dependent on, civilization, namely, the transmission of helminths through the active agency of insects. The outstanding instance, of course, is filariasis. This is independent of food, sanitation, and clothing—unless, indeed, the whole body, including the face, could be covered. Even here, however, a means has been found to limit the occurrence of the disease—namely, by filling up the swamps and marshes, and thus destroying the breeding grounds of the mosquito. This measure might well enough be included under sanitation. These, then, are the main prophylactic and preventive measures, and, could they be efficiently carried out in all cases, man would cease to be afflicted with helminth parasites. This, certainly, is a counsel of perfection, and it seems vain to hope for its ultimate attainment in tropical countries. So long, however, as it fails of complete realization, just as long will there be helminthiasis in these regions. Medicinal remedies in places where helminthiasis is endemic are of merely transient utility. They only touch the outcrop in various isolated individuals, all the while the root of the evil remains untouched. Here, assuredly, one effort directed towards prophylaxis is worth a hundred towards cure.

ON RECURRENT MOTOR PARALYSIS IN MIGRAINE,

WITH REPORT OF A FAMILY IN WHICH RECURRENT
HEMIPLEGIA ACCOMPANIED THE ATTACKS.

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RECURRENT paralyses in some of their varieties have recently attracted considerable attention.¹ In migraine an opportunity for observing such paralysis is very rare, for it is a commonplace that the symptoms in the great majority of attacks of migraine are exclusively on the sensory side. In what follows I propose to give an account of a family in which hemiplegia, with, as a rule, loss of speech, was a constant feature of attacks of migraine, and to such a degree as to be almost unique, so far as I can ascertain; and also to deal with the forms of motor paralysis which occasionally occur in this disorder.

The restriction of the attack to purely sensory phenomena is one of the most interesting features of migraine, and at the same time one of the most puzzling. In an affection like migraine, of which the exact cause is unknown, and in which there are no recognizable pathological changes, the diagnosis rests upon the symptoms and their grouping. As a rule, the peculiarity of the symptoms and the regularity of their order of occurrence make the affection as definite as any symptom-group in medicine. But in diseases where the diagnosis depends upon the symptoms it is essential that these should conform to the accepted type. This is especially the case when phenomena are present over and above those recognized as proper to the attack. In some cases of migraine which lie on the borderland between it and other neuroses the distinction is by no means easy, and sometimes must be left in doubt. Especially may such difficulty arise in deciding between a diagnosis of epilepsy and migraine.

In the family history given below the strongly hereditary character of migraine is well marked, and also the tendency to direct transmission of the disease. The characters of the attacks which mark them as belonging to migraine will, however, be better considered when the cases have been described.

Attacks of migraine may be associated with motor paralysis in several ways, excluding those cases in which it occurs in accidental association with independent organic brain disease, such as tumour, or in which it is doubtful whether atypical migraine does not belong to another affection such as epilepsy.

1. *Migraine Secondary to Structural Lesions.*

Attacks of migraine may be a symptom of onset in hemiplegia due to a vascular lesion or to an intracranial

tumour. This group I do not propose to consider. In connexion with the production of an attack of migraine by occlusion of an artery it may be recalled that Leonard Hill² produced an attack in himself by digital compression of one carotid artery.

2. *Long Standing Migraine Complicated by Paralysis.*

Cases in which migraine of long standing has issued in permanent paralysis, generally due to a vascular lesion. In some of these one of the phenomena of the aura of the attack, such as aphasia or hemiopia, has become permanent, but in others the permanent disability in no way corresponds to the aura. Instances of this kind are fairly numerous.

In a case reported by Oppenheim,³ in a patient who suffered from old-standing migraine, there occurred in the course of an attack stupor with persistent aphasia and right hemiplegia, found to be due to thrombosis of the internal carotid at the origin of the Sylvian artery.

In Infeld's⁴ case, a woman aged 27, who suffered from hereditary migraine, in one attack felt something give way in her head, and fell but did not lose consciousness. There resulted right hemiplegia, with hemianaesthesia and blindness of the right eye. One month later there remained weakness and spasticity, with post-hemiplegic disorder of movement and slight paraesthesia.

J. J. Thomas⁵ gives two cases, in one of which an attack like migraine was followed by left hemiparesis, hemianaesthesia, and hemiopia; in the other, a woman aged 27, subject to migraine, left hemiparesis, hemiparaesthesia, and hemiopia resulted. In both cases hemiopia was permanent; the other symptoms cleared up. He gives another case of migraine in which permanent hemiopia resulted.

Indeed, hemiopia as a permanent result of migraine seems to be more common than paralysis, although both are fortunately rare. Often in these cases the hemiopia forms a very marked feature of the aura preceding the attack,⁶ but this, as stated above, is by no means invariable. In one case under my care a woman, aged 35, had suffered for seventeen years with attacks of migraine preceded by right hemiopia. One morning she woke up with dimness of vision for objects to the right, and this in the course of a week developed into right hemiopia, which remained permanent. The optic disc looked pale, but was otherwise normal. Her vessels were healthy.

With regard to such cases as the above, those who believe that attacks of migraine are due to vasomotor spasm of cerebral vessels have raised the point whether constantly repeated spasm of an artery may not in time lead to disease of its walls, and hence to rupture or thrombosis. It is difficult to speak with certainty on this point, but the great infrequency of permanent paralysis in a disease so common as migraine, the fact (at any rate, in my experience) that sufferers from migraine do not suffer in greater proportion from atheroma or arterio-sclerosis than other persons not so affected, and the fact also that such paralysis when it occurs often affects persons under 40—the age of the patients mentioned above is noteworthy—are all against this view. There must, in addition to migraine, be some other factor at work. Further, as Spitzer⁷ points out, if repeated vasomotor spasm led finally to thrombosis it would be expected that the finest arterial twigs would be affected, whereas in some of the recorded cases large vessels must have been involved. Exception to this last statement should be made for a few cases in which there was good evidence of thrombosis of the central artery of the retina.

J. J. Thomas⁸ states the case very fairly by concluding that migraine may occasionally result in permanent paralysis, aphasia, or hemiopia, and that in most instances this is due to an attack favouring a vascular lesion in persons who already have disease of the vessels, but that in others the lesion may occur in young persons whose blood vessels are in all probability in a normal condition; and that although great caution is necessary, before ascribing such paralyses to migraine, to exclude coincident and independent disease—for example, of the vessels—yet a few cases remain which justify the statements made by Charcot and others that the normally transient hemiopia or aphasia may become permanent.

3. *Migraine Attended by Temporary Paresis.*

Cases in which paresis or even paralysis, temporary and recurrent, is one of the regular phenomena of the attack. In the ordinary way this consists of slight motor weak-