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With Special Reference to British and other European Forms

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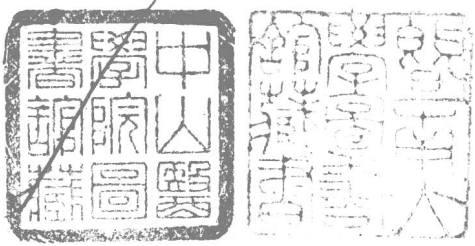

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PREFACE

The growing importance of Helminthology during the past two or three decades has been indicated by the publication of several text-books on the subject. Some of these books deal in part with trematodes, but only with a few forms of medical or veterinary interest. For a much longer period of time than that the detailed study of the Trematoda has been sadly neglected in Britain, and zoologists interested in the group have been obliged either to search for information in foreign periodicals, or to take what they could find in a few standard works in German and in the *Oxford Treatise*, the *Cambridge Natural History* and ordinary text-books of Zoology. In writing a book with the hope that it will fill this gap in our scientific literature my aim has been to make available in English, and in a single volume, information that will enable students, teachers and research workers of Zoology in our schools, colleges and universities to identify the trematode parasites of representative animals from the European fauna, and also to provide a broader outline of the structure, modes of life, bionomics and life histories of these animals than can be found in any one book hitherto published in any language. I have not been able to satisfy fully the requirements of specialists, but I have tried as far as possible to indicate where they can find the information they seek.

Parasitism figures prominently in the zoological curriculum at the present time and it is a topic that can be illustrated fully by the study of trematodes, which rarely fails to arouse an enthusiastic interest in students. As a student and university teacher for more than twenty years I have found my wonderment at the phenomenon of parasitism undiminished but, like many other persons, I have been impressed also by the difficulties of naming specimens and finding out what is known about them. The reason for this has been a very extensive literature of original papers written in various languages and dispersed in periodicals so as to be difficult of access. Only about one-half of nearly sixteen hundred papers mentioned in my list of literature are written in English, and most of the many older papers excluded from the list are written in some other language. No doubt many students of Zoology have had their potential interest in the Trematoda stifled at the source by such difficulties as were encountered during the quest for relevant information about the members of this class.

It was perhaps imprudent of me to compile a book such as this during a period of total war, for circumstances during the war years did not favour intensive laboratory work and many journals were especially difficult to consult because put out of reach in places of safety. My task could have been carried out with less trouble and better results in normal times, but it may be taken to represent my unwillingness to relinquish academic research as a supplement to my teaching duties solely on account of enemy activity. Much of the writing

was done, many of the figures drawn, during the period when air raids were harassing Bristol and London, and in both these cities. My scientific conscience was consoled by this and other responses of the same kind to enemy action at a time when even teaching work could hardly be guaranteed from one day to the next. Acutely conscious of many defects in my work, I can claim to have striven to attain accuracy in regard to factual matter as far as checking and rechecking can make this so. I have made a special effort also to use scientific names as they ought to be used and to eradicate the confusion that has in some instances resulted from their misuse.

Several friends have given me encouragement and help of some kind or other at all stages of my work, and to all those who have in any way prevented me from relinquishing my set purpose I proffer sincere thanks. Professor D. L. MacKinnon has been patient beyond belief with what must have been my very irritating preoccupation with a special branch of Zoology. Professor C. M. Yonge showed a perennial interest in my work and I was extremely fortunate to have the pleasure of working in his well-regulated Department of Zoology at Bristol. He made me a loan of several specimens and a number of reprints and he never missed an opportunity to ease my task with appreciative words and actions. In the matter of obtaining periodicals the Librarians of King's College and the University of Bristol gave me unstinted assistance, and both they and their assistants were unbelievably courteous in the face of extortionate requests. My thanks are due also to the Librarian of the Linnaean Society, for both he and his assistant enabled me to consult numerous papers that were unobtainable elsewhere. Dr H. E. Baylis richly deserves my special thanks for the loan of many reprints from his extensive collection and also for much invaluable criticism and advice. He read through the draft of my manuscript at an early stage of its preparation, but in fairness to him and to indicate that he has in no way condoned any errors that may be found in my book I must add that many additions have been made without his cognisance. I am very grateful to him for the time he devoted to my work and for his esteemed counsel. I owe a large debt of gratitude also to my dear friend H. C. Dyer, whose assistance and encouragement were available to me at all times. I am grateful also to the Cambridge University Press for the care they have lavished over the production of my book, and especially for the great skill of their proof-reader, who has saved me from many errors and inconsistencies.

Lastly, I gratefully acknowledge the contributions that have been made to my book by zoologists too numerous to name here but named in chapter 16, for their researches have provided the fund of knowledge from which I have drawn substantially. I have tried to bear in mind the need to give credit where it is due and if, inadvertently, I have failed to make suitable acknowledgement in any place I can only point to the list of literature given and acclaim my indebtedness to all persons whose names are included therein. Some of my

figures are original, but many have been redrawn from those of writers whose names are given, and I am glad to acknowledge here the debt of gratitude I owe to them. My best efforts to do justice to the vast amount of material at my disposal have been inhibited in some instances by the need to keep the size of the book within bounds, but I shall welcome any criticisms, statements and specimens which might improve the book for the working zoologist if and when revision becomes necessary. The need for further research is evident on nearly every page of the book, and it is my earnest hope that British zoologists may be stimulated in one way or another to work towards a better understanding of the interesting animals with which my book deals.

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CHAPTER 1

THE PHYLUM PLATYHELMINTHES

The large and varied assemblage of multicellular animals or Metazoa which constitute the phylum PLATYHELMINTHES is arranged in three classes, Turbellaria or planarians, Trematoda or flukes, and Cestoda or tapeworms. A few forms with indubitable platyhelminth characters do not fit easily into this scheme and are placed in a fourth class called Temnocephalida, which is intermediate between Turbellaria and Trematoda. Some zoologists place the ribbon-worms or Nemertini in the same phylum as the flatworms and, certainly, there is an affinity between the two kinds of worms. But in some respects, notably in their unisexual nature, nemertines are simpler than platyhelminths, and in others, especially the occurrence of a blood-vascular system, they show great advance beyond the typical flatworm organization, so that we are justified in placing them in a different phylum. Roundworms or Nematoda are sometimes grouped with flatworms under the name 'helminths', but they too belong to a phylum with which we are not concerned.

Superficially, the four kinds of flatworms seem to have little if anything in common. They differ so much in appearance, structure and mode of life that it is not easy to formulate the general characters of the phylum as a whole. Sometimes the body is covered with delicate protoplasmic threads or *cilia*, sometimes with a layer of non-living, secreted material or *cuticle*. The digestive system may be elaborate, or not a vestige of it may remain. Male and female reproductive systems may exist in the same individual or, very rarely, in separate individuals. The external surface of the body may be complicated by the existence of various kinds of adhesive organ, or simple as a result of their absence. Differences in the mode of life and life history may suggest not affinity so much as the negation of it.

In spite of these differences, Platyhelminthes have much in common. They are bilaterally symmetrical, i.e. one side of the body resembles the mirror image of the other; the tissues originate from one or another of the three primary germinal layers, ectoderm, endoderm and mesoderm, which develop in the embryos of all animals of higher status than Coelenterata in the animal kingdom; the body lacks a central cavity or *coelom* and a blood-vascular system, the internal organs being enveloped in a spongy packing tissue or *parenchyma* which originates from mesoderm; the principal muscles of the body form a tube several layers thick immediately beneath the integument. Further, the excretory system, by which waste materials are assembled and expelled from the body, comprises in all of them a system of fine canals and finer branches, each of which ultimately terminates in a special kind of cell called a *flame cell*. This has long cilia which project into the lumen of one of the ultimate excretory canaliculi and by their lashings present a flickering appearance, as the name implies. Add to this and the foregoing characters the androgynous nature of most flatworms and the fact that when a digestive system exists it has a mouth, but rarely an anus, and the distinctiveness of the phylum is clear.

(*a*) *Turbellaria*. Planarians are so called because they are flat, unless the name has something to do with Gk. πλανάω, meaning to lead astray or wander. The corresponding scientific name Turbellaria signifies a particular kind of flatworm, the activity of which sets up disturbances or *turbellae* in the watery surroundings. These eddies are created by the lashing motion of innumerable cilia which cover the body, arising from a sheet of cells or *epithelium* at its surface. Other kinds of flatworm lack cilia when adult, but may possess them during the early development. There is no sign of a cuticle in the integument, but the epithelium contains secretory cells which form rod-like bodies called *rhabdites*, and these are extruded and swell in water to form an investing slime which aids ciliary locomotion. Other distinctive characters of the Turbellaria are the position of the mouth behind the brain, the lack of thick-shelled eggs, and the direct nature of the development.

Unlike adult flukes and tapeworms, most planarians live in freedom, many in the sea, others in ponds and streams, and some in damp situations on land. They hunt and devour living prey, the large land planarians thus despatching earthworms, snails and woodlice. Not all planarians preserve such independence, however. Some have come to live in habitual association with molluscs and echinoderms, and a few have acquired the habit of penetrating into and living in the bodies of sea-urchins, holothurians and other invertebrates, thus foreshadowing the parasitic ways of all flukes and tapeworms.

(*b*) *Trematoda*. A trematode or fluke habitually nourishes itself at the expense of another animal, called the *host*. Many trematodes attach themselves to superficial parts of the host, but many others penetrate into the body and settle down in one of the internal organs. The former are called *ectoparasites*, the latter *endoparasites*. The life history provides a more important distinction. Ectoparasitic trematodes develop directly in or on a single type of host and are said to be *monogenetic*; endoparasitic trematodes develop through a sequence of young individuals unlike the parent (*larvae*) with at least one and sometimes more than one change of host, and are said to be *digenetic*. As a rule, digenetic trematodes spend a good part of their larval life in the bodies of molluscs, and some leave the first host and penetrate into another mollusc or a crustacean, or sometimes a fish, before finally settling down in a vertebrate animal to become mature. The vertebrate which harbours the adult fluke is called the *final* host; the invertebrates which succour the larvae and the vertebrates which shelter only juvenile individuals are called *intermediate* hosts, of which a given trematode may thus have one or more than one.

Most trematodes are flattened creatures ranging in size from a minute speck to a length of several inches. They cling to the host by means of special organs of adhesion and anchorage, generally suckers but often hooks, and sometimes both. The cavities of the suckers superficially resemble perforations of the body, a false character to which the name *trematode* refers. Some trematodes browse on mucus extruded from the tissues of the host, others imbibe fluid nutriment by suction from organs like the intestine, and some tackle the tissues themselves, causing their breakdown and resulting in serious injury to the host. Only rarely, however, are the demands of the parasite too heavy to be borne by the host without serious threat to its well-being.

As a rule, trematodes have several other distinctive characters in common. The outermost layer of the integument generally lacks both an epithelium and rhabdite-containing cells, and forms a cuticle. There are no tentacles, though papillae may exist in some regions, notably near the foremost (*anterior*) extremity. The mouth is situated far forward at the tip of the body or near it on the lower (*ventral*) surface. The digestive system is well developed, and generally the intestine is bifurcate. The eggs are encapsulated. The *ensemble* of characters serves to distinguish the trematode from all other kinds of flatworms, including the Temnocephalida.

(*c*) *Cestoda.* Tapeworms and their allies are invariably endoparasitic, and with few exceptions, notably *Archigetes*,* which lives in fresh-water earthworms, attain maturity only in the alimentary canal of a vertebrate animal. When fully grown the cestode may be a mere tenth of an inch long, or, at the opposite extreme, it may attain a length of several yards. This kind of flatworm has undergone extreme modification as a result of long-sustained parasitism in its ancestry, but is simplified in structure rather than degenerate. Only organs which are essential to a comparatively safe and easy existence have been retained. At one end of the worm a *head* or *scolex*, provided with suckers or hooks or both, enables the animal to secure and maintain a hold on the intestine of the host and safeguard itself against a constant threat of expulsion. Behind this a short *neck* of embryonic tissue propagates a long chain or *strobila* of rectangular segments or *proglottides*. Some cestodes are "unsegmented" and without a scolex, and can easily be mistaken for trematodes, but in tapeworms the strobila may consist of more than a thousand proglottides, each of which has at least one set of male and another of female reproductive organs. Apart from this elaboration the structure of the tapeworm is simplified. The body is covered with a cuticle, which generally lacks spines or other appendages. There is no digestive system, all nutriment being imbibed through the integument. Other systems of organs show a low grade of organization, though the nervous and excretory systems are well developed, and the parasite is little more than an efficient machine for producing innumerable eggs. Fecundity is an essential characteristic of Cestoda, as it is of endoparasitic Trematoda, both classes of flatworm being faced with great hazards during the period of larval development, when they have to establish themselves in a sequence of fresh hosts.

(*d*) *Temnocephalida.* Temnocephalids attach themselves to the surface of an invertebrate animal, generally a fresh-water crustacean, but they do not derive nourishment from their 'host'. Instead, they capture and devour insect larvae, rotifers and other small creatures which abound in the surrounding water, and are thus not parasites in the full sense of the term, but merely passengers. In their habits they have more in common with Turbellaria, with which they are linked in some schemes of classification, than with other Platyhelminthes. But they show some structural conformity with Trematoda, having a posterior sucker and a hermaphrodite reproductive system of similar general plan. The gut is simple and saccular, as in some Turbellaria and a few Trematoda, and it opens by a mouth but lacks an anus.

* According to Szidat (1937*b*), *Archigetes* is the neotenic larva of *Biacetabulum*, whose adult lives in fishes.

Despite these resemblances to other classes of flatworms, Temnocephalida are easily distinguished from Trematoda. There is no typical external ciliation in either class, but in the former there is a superficial epithelium containing rhabdite-forming cells and cilia may occur in patches or localized regions in exceptional instances. Eyes occur more frequently than in Trematoda, where they are confined to the larval stages, except in a few monogenetic flukes. The mouth is situated on the ventral surface, more widely removed from the anterior extremity than in trematodes, and the truly distinctive character* is a circlet of at least four and as many as twelve tentacles at the anterior end of the body. Their epithelium contains abundant rhabdite-forming cells. Another distinctive character, though a negative one shared with Turbellaria, is the lack of thick-shelled eggs.

This preamble serves to show that the four classes of the Platyhelminthes can be distinguished by comparatively simple characters of practical importance. The first step in the separation of adult flatworms is to determine the nature of the integument. If it is completely ciliated, there is a clear indication that the worm belongs to the Turbellaria. There is some risk of the loss of the superficial epithelium in a badly preserved turbellarian, but other characters are available and would be utilized in any case to confirm the tentative diagnosis. A flatworm which lacks external ciliation or is ciliated only in patches, but has an epithelial integument, must belong to the Temnocephalida, a diagnosis which is confirmed by the presence of anterior tentacles and a posterior sucker. The existence of suckers on the cuticularized surface of a flatworm with a well-developed digestive system clearly indicates trematode affinities. The lack of a digestive system in an adult flatworm with a cuticle just as clearly signifies cestode affinities. It would be unwise to examine only these elementary characters, but they are obviously the first to be considered.

Mistakes are easily made and the student is forewarned. *Myzostomum* was believed to be a trematode till the great helminthologist Leuckart showed it to be an annelid; *Pentastoma* was included in this class till P. J. van Beneden discovered its embryo and allocated it to the Arthropoda; *Phoenicurus* Rudolphi, 1819† was declared a cestode parasitizing the mollusc *Tethys* till it was proven to be merely an appendage detached from that animal. Perhaps the likeliest source of error parallels that by which *Thysanosoma* was first described as a trematode, though in reality a proglottis detached from the strobila of a cestode. Free cestode proglottides frequently occur in the intestine of fishes, one location in which trematodes are sought. It is good policy to examine the credentials of a suspected parasite whilst it is alive, because the translucency of the living body permits observations to be made of even the finest details of structure (see the Appendix).

* The most notable exception is *Bucephalus polymorphus*, a digenetic trematode belonging to the Bucephalidae, which could never be mistaken for any other kind of flatworm.

† *Phoenicurus* Forster, 1817 is a bird, the redstart.

Monogenea, Aspidogastrea and Digenea, the Orders of the Trematoda

Most trematodes are pale cream in colour, but some acquire a distinctive coloration from the nutriment which they extract from the host. Those which include blood in their diet are tinged red when alive and have brown intestinal contents when preserved. Often the eggs are yellow or golden brown, and when they are numerous the parasite gains further coloration from them. Few trematodes have intrinsic colour, but some larvae possess distinctive pigments, most cercariae of the *Rhodometopa* group being tinged pink.

Size is an important criterion in the classification of Trematoda. Many flukes would be overlooked if we confined our attention to trematodes as large as the well-known species *Fasciola hepatica* or *Polystoma integerrimum*. Most trematodes are less than 30 mm. long, but very large species like *Fasciola gigantica* and *Fasciolopsis buski* may attain a length of 75 mm. and a breadth of 15 mm. At the other extreme, *Heterophyes heterophyes*, the smallest trematode parasite of man, never exceeds 2 mm. in length and 0·7 mm. in breadth. Taking the third dimension into consideration also, evidently some flukes are one thousand times as large as others. The size of a trematode is not known to be correlated with that of the host, but this is not to say that the host is without influence on the growth of its parasites. It seems likely that an internal parasite will be influenced by substances which circulate in the body fluids of its host, but there is a marked hiatus in our knowledge of such matters and little information on the general problem of trematode growth.

Size might be a misleading criterion of distinction were it carelessly applied, because living Trematoda have neither a fixed final size nor a constant shape. The continual play of antagonistic muscles shortens and thickens the body, or alternatively lengthens and attenuates it, considerably modifying its apparent size and shape. Careless fixation may perpetuate one of a number of momentary poses and give a distorted impression of what might be called the mean size and shape. But careful fixation generally provides a specimen of typical form. Difficult as it is to ascertain the sizes of different trematodes, there is no doubt that size is an important character, and in defining it in the following pages I shall use consistently a scheme which was formulated by Lühe, but which has been slightly modified, assuming that the measured parasite was neither unduly extended nor markedly contracted.

Scheme of Size Terminology

Term denoting size	Length of the body (mm.)	Term denoting size	Length of the body (mm.)
Very small	0–1	Fairly large	12–20
Small	1–3	Large	20–35
Fairly small	3–7	Very large	35
Medium	7–12		

Some characters by which the three orders of trematodes are distinguished are so elementary that scrutiny of external structures and apertures on the surface of the body will permit a broad diagnosis to be made. Generally, the mouth is at or near the anterior extremity, though in some trematodes it is near the middle