# The Significance of Studies on the Life Histories of Animal Parasites with Special Reference to Some Digenetic Trematodes*

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Although animal parasites and some of the diseases they cause were recognized before the Christian era, almost all we know about their life histories has been determined since the middle of the 19th century. The first tapeworm and nematode cycles were traced in the 1850s by Küchenmeister, Leuckart, and Herbst. About this time, some very accurate surmises were made concerning the life history of digenetic trematodes. It is a little startling to read the works of Steenstrup and Moulinié with the knowledge that they were written over a generation before Leuckart and Thomas independently demonstrated for the first time the life cycle of a digenetic trematode, *Fasciola hepatica.* Although the part played by insects in the spread of certain helminth infections was demonstrated in the 1860s, the essential rôle of arthropods in the transmission of protozoan parasites was not proved until 1893 when Smith and Kilbourne demonstrated that ticks transmit the causative agent of Texas Cattle Fever. This epochal discovery was the first in a rapid series demonstrating the part played by arthropods in the spread of such important diseases as malaria, yellow fever, trypanosomiasis, bubonic plague, typhus, and dengue fever. Today, malaria alone takes a greater toll of human life and efficiency than any other infectious disease; this fact is becoming increasingly appreciated by those responsible for the health of our armed forces on battle fronts of the South Pacific and the Mediterranean. Truly it may be said that no other two decades in the history of zoology approach the years 1890 to 1910 in their contribution toward our knowledge of the causes of human suffering and mortality.

During the present century, application of the experimental method to the solution of life histories has received more and more emphasis. As a result, a great many new life cycles have been traced and hitherto obscure aspects of known cycles have been elucidated.

The most obvious and impelling reason for such studies is the control of diseases of man and the animals he has domesticated. Knowledge of the life history of a parasite reveals the point at which the cycle may be broken as a chain at its weakest link. This is an all important consideration in controlling such diseases as trichinosis and fowl coccidiosis for which effective treatments are as yet unknown. The use of knowledge gained from life history studies, then, is nothing more or less than preventive medicine.

It is generally supposed that we now know the life histories of practically every animal parasite of any consequence to the health of

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man and domestic animals. That is largely true as far as the identity and means of transmitting such parasites are concerned. There are, however, in many life cycles, important questions which have not been answered satisfactorily. For example, what becomes of the malarial sporozoite after it is injected into the blood stream by the proboscis of the mosquito? Textbook figures show it entering red blood corpuscles, directly initiating the schizogonous cycle in the circulating blood. As far as I know, no one has ever seen this happen; as a matter of fact, it is impossible to demonstrate the presence of malarial parasites in peripheral blood for a considerable time after the mosquito's bite.

One might ask—in fact, it has been asked—if studies on the life histories of parasites of lower animals are not being overdone. After all, does not every digenetic trematode, for instance, have about the same general type of life cycle including an adult stage in a vertebrate host and larvae that develop in some species of mollusk and manage to get back to the vertebrate by one means or another? Has not just about every conceivable means of such reentry been described? If, as known life histories indicate, related parasites have parallel life histories with similar hosts and similar means of getting from one host to another, why clutter the literature with further papers which contribute little more than a confirmation of this thesis? These are fair questions and ones upon which I trust the ensuing remarks may have some bearing.

Not infrequently, the understanding of the life cycle of an important human parasite has been preceded or greatly facilitated by the elucidation of the cycles of closely related forms occurring in lower animals. Ross traced the malarial cycle in birds before it was followed in man. An answer to the question already raised concerning the early stages of human malaria may be facilitated by the recent discovery of a bird malarial parasite which infects cells of the reticuloendothelial system instead of circulating blood corpuscles. This discovery may also throw much light on the mystery concerning relapses of malaria after parasites have apparently disappeared from the patient's blood stream. Thus have studies on the life cycles of parasites of lower animals implemented and supplemented our understanding of related parasites of man. Aside from the fact that lower animals are more cooperative than man as experimental subjects, studies of life cycles demonstrate that the same fundamental principles and phenomena characterize a related group of parasites regardless of their hosts. It therefore is unwise if not indeed impossible to separate medical and veterinary parasitology from the purely zoological aspects of the subject.

The fact that one or more life histories in a family of parasites may be known should not discourage further investigation of that group. The next cycle that is traced may yield some surprising and significant results as I shall show by examples taken from recent studies on the life histories of some digenetic trematodes, the group with which I happen to be the most familiar. A few introductory remarks will relieve the abrupt "jump" to these parasites.

Before many life cycles were known, the Digenea were separated into groups based necessarily on such adult characters as adhesive

organs and nature of the digestive, reproductive, and excretory systems. The adhesive organs, i.e. suckers, were used to separate the Digenea into suprafamilial categories, the monostones, holostomes, amphistomes, distomes, and gasterostomes. While this distinction still has certain usefulness, its artificiality became apparent with more precise studies of internal anatomy and has been abundantly demonstrated by life history studies. These have shown, for example, that certain monostomes are more closely related to amphistomes than to other monostomes and that some distomes are nearer holostomes than other distomes. It has even been found in one instance that the immature stage of one monostome is distomatous and that the ventral sucker degenerates as the worm becomes sexually mature. Organs of attachment, then, are interpreted as adaptations to parasitism and hence are not primitive characters providing trustworthy indications of relationships. The digestive and reproductive system likewise have been subject to profound modifications in becoming adapted to the parasitic habit and have mislead investigators in their attempts to devise a natural classification. In recent years, the excretory system has received much attention as a basis for the classification of trematodes since it would seem to be the most conservative system and therefore least altered in adaptation to parasitism. Indeed it does seem that most profound changes in the physiology of the organism would have to occur before its excretory function would be greatly altered. The flame cell arrangement is similar in related trematodes and empirical formulae have been expressed for the patterns in the various families. Yet such formulae do not consider the embryological development of the excretory bladder and its post-embryonal modifications. Furthermore, the same excretory formula may apply to more than one family and not hold for all members of the same family. It must be concluded then, that in some cases at least, distantly related adult trematodes have come to resemble one another so closely that one not familiar with their life cycles would be deceived by their mutual resemblance. Some instances suggest that this convergence may be the result of long inhabitation of the same or similar hosts. One may cite, for example, the large group of trematode parasites which occur in fishes and look so much alike that they were long believed to constitute a single family, the Allocreadiidae. While the interrelationships in this group are not yet clear, life history studies indicate that it is a heterogeneous combination of at least three distinct families.

The basis for this conclusion and for determining the relationships of trematodes in general is the fundamental zoological principle of recapitulation. Although this time-honored concept has been severely criticized in some quarters—a manifestation of the "debunking" epidemic of the twenties and thirties and no respector of either national heroes or scientific theories—there is good reason to expect that it and it alone will serve as the ultimate foundation for an enduring natural classification of the trematodes and many other parasites as well. The principle that closely related trematodes have similar hosts, embryological development and larval stages can be applied only with the aid of precise life history studies. The interpretation of larval stages must be made with

caution, however, for they as well as adults may possess misleading secondary modifications and will be shown presently.

We may now consider some examples of how the knowledge of life histories has altered our conception of certain families of digenetic trematodes. The family Acanthocolpidae was proposed to contain certain trematodes living in the intestine of marine fishes and having in common, among other characteristics, peculiar modifications of the genitalia. It has been known for several years that fish become infected with these flukes by eating other fishes containing the encysted metacercarial stage. Then Martin traced the life history of *Stephanostomum tenue* and showed that this member of the family has a rather uncommon type of cercaria which develops in a marine prosobranch snail and has a simple tail, eye-spots, and a stylet. Cercariae escape from the snail and penetrate fishes. Since this is in agreement with earlier observations on encysted stages, it seemed likely that all members of the family would have life histories quite similar to that of *Stephanostomum tenue*, i.e., have ophthalmoxiphidiocercariae which encyst in fishes. Later Dr. Hunninen and I traced the life history of *Deropristis inflata*, a charter member of the family Acanthocolpidae. To our surprise, we found that the cercaria of this species was quite different from that of *Stephanostomum* and encysted in annelids instead of fishes. Consequently, it was necessary to revise the family and transfer *Deropristis* to another where, judging from adult characters, one would never have supposed it belonged.

Another example of the misleading resemblance of adult characters is afforded by the Microphallidae, formerly included with the Heterophyidae because of the apparent similarity of their genitalia. As a matter of fact, this resemblance is superficial and there are in both groups all stages from the most modified genitalia to the generalized type characteristic of many other trematodes.

Not only may trematodes of different families possess misleadingly similar modifications of the genitalia but also two members of the same family may differ widely in this and other respects. This difference is well illustrated by the opecoelid genera *Opecoeloides* and *Podocotyle*. In *Opecoeloides*, there is no cirrus sac, a small accessory ("genital") sucker is situated on the forebody and the intestinal crura open into the excretory vesicle, the excretory pore thereby serving as an anal opening. *Podocotyle*, on the other hand, has a well developed cirrus sac but lacks the accessory sucker and connections between the digestive and excretory systems. Yet these trematodes have cercariae that are almost indistinguishable, identical excretory patterns, and exactly parallel life histories. Those not familiar with the trematodes may be surprised to learn that some members of the group possess anal openings and may be inclined to attach considerable significance to their presence. Ozaki proposed three distinct families based almost solely on the various types of these openings. However, several investigators have disagreed with this view and their opinion that anal openings in trematodes are secondary structures with no greater than generic value has been abundantly substantiated by life history and morphological studies.

One example will suffice to show that additional life history investigations in groups that have already been studied to a considerable extent may yield pertinent information concerning the relationship of one family of trematodes to others. Several studies have demonstrated that the cercarial stage of the Brachylaemidae is either tailless or possesses a very minute tail. From the number of such studies, it might be supposed that these are the only types of larvae that members of the family would possess. Allison has shown very recently, however, that one member of the family has a typical fork-tailed cercaria which is free swimming. This study indicates that in the other known brachylaemid cercariae, rudimentation and loss of the tail is associated with the suppression of a free swimming phase in the life history. The extreme of this modification is seen in *Leucochloridium* whose cercarial stage does not leave the snail at all but remains in the sporocyst which grows into the tentacles of the snail. As a result, the tentacles become enlarged and brilliantly colored, resembling caterpillars. These attract the attention of birds which pick off and eat the tentacles containing the worms, thereby becoming infected. Interesting as this life history is, the discovery of a fork-tail larva in the family is more important for it immediately suggests that the group is related to others having similar larvae. Yet had it been assumed that a knowledge of the life histories of three or four other members of the family was sufficient—that further study would be a mere repetition—this significant discovery would not have been made.

This example also illustrates the caution that must be exercised in the interpretation of larval stages. Caudal rudimentation and other secondary modifications of larval stages must be recognized for what they are. It is obvious that the more life histories we know in a group, the easier it becomes to determine with certainty the primitive or typical larval type and understand the nature and extent of secondary modifications. In several families of trematodes, there seems to have been a shortening of the life cycle with the gradual elimination of the second intermediate host which enables the parasite to get from the mollusk to the definitive vertebrate host. This tendency is illustrated by some of the microphallids. The cercaria of *Spelotrema nicolli* has a well developed tail by means of which the larva swims actively after escaping from the snail. We have found a closely related cercaria, as yet undescribed, which has a tail about half as long as that of the *Spelotrema* cercaria, and although it escapes from the snail, this larva is utterly incapable of swimming. Rothschild has found, however, that another microphallid larva develops a tail but sheds it and encysts without even leaving the snail. This species accordingly has only two hosts in the cycle, the snail and the vertebrate which becomes infected by eating the snail. Microphallid cercariae that escape from the snail, however, have a third host in the cycle, a crustacean into which the cercariae penetrate and encyst.

The above disussion has emphasized mostly the usefulness of life histories for taxonomic purposes. The broader implications of such studies should be mentioned at least. Although life history studies, if well done, include many minute details and presuppose an acquaintance

with a considerable amount of literature if effort is not to be misdirected, they are far from narrow, specialized investigations. If, for example, one undertakes tracing the life history of a digenetic trematode, consideration must be given not only to the parasite itself but also to the structure, habits, ecology and distribution of the molluscan and vertebrate hosts and very likely a second intermediate host belonging to a still different class of animals. If, as is usually the case, one begins with a knowledge of only one stage and its host, the chances are that the acquaintance of a number of animals will be made before the other hosts are determined and the cycle proved. The study of trematode life histories may be a slow way to become familiar with the fauna of a locality but I know of no method that is more interesting or demonstrates in a more impressive manner the incessant struggle for existence and impact between organisms in the web of life.

Life history studies indicate with considerable clarity that complex cycles involving two or more hosts evolved very slowly, including at first a single host to which others were added gradually, one at a time. Life history studies suggest, for example, that ancestors of the malarial *Plasmodium* and the trypanosomes first parasitized and developed fairly complex stages in invertebrates alone, possibly before the appearance of vertebrates. These ancestral parasites must have evolved along with their hosts, their descendents becoming parasites of their hosts' descendents, new species arising to parasitize new host species. With the evolution of blood sucking habits among some of these invertebrate hosts, a portion of their parasites' life cycles was bestowed upon the vertebrates which provided the blood meals. Most of the invertebrates, however, did not become blood suckers but some of these fell prey to other animals with whom they shared their parasites. Thus have sporozoans and flagellate parasites taken advantage of the habits of both predators and blood-suckers in extending their life histories to include more than one host. Some of the relatives of the ancestral *Plasmodium* and *Trypanosoma* did not take this step, however, and their descendents have remained one-host parasites until this day. It is significant that some of them have essentially the same stages in one host that their relatives have divided between two host species.

In brief, it may be stated that the study of parasite life histories is a study of the way of life practiced by the majority of living things. It is an inquiry into the manner in which they assumed that way of life, have become adapted to it, and have taken advantage of the associations and habits of other organisms. Finally, it exposes the risks inherent in the parasitic mode of life and reveals means of increasing the risks for those who by choice or necessity live at the expense of others.