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Edited by

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Advances in
PARASITOLOGY

VOLUME 11

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PREFACE

This book, the eleventh of the series, contains nine full reviews by ten writers, who deal with various kinds of parasites (trypanosomes, monogenetic and digenetic trematodes, acanthocephalans, cestodes and nematodes) and also with some broad parasitological problems such as imported parasitic disease, the control of arthropods of medical and veterinary importance, and the effects of population density on the growth and reproduction of snail vectors of a schistosome parasite of Man. Short updated reviews deal with malaria in mammals excluding Man, *Toxoplasma* and toxoplasmosis, the biology of the Acanthocephala, and the post-embryonic development of cestodes. The writers of these reviews live in Britain, Czechoslovakia, Canada, U.S.A. and Australia.

John E. Bardsley and Rudolph Harmsen have made a detailed study of the trypanosomes of tailless Amphibia (Anura), an area of research in which knowledge can be gained about the evolution of trypanosomes. The fact that arthropods serve as vectors in a group predominantly "vectored" by leeches may be an example of "evolution in action". Ten main sections of the review deal with taxonomic and phylogenetic considerations, morphology, electron microscopy and cytology, life cycles, distribution, the vertebrate host and pathogenesis, physiological processes, the invertebrate host, and media, physiology and biochemistry applied to methods of culture. Three useful tables are provided: one is a list of all published specific and subspecific names of anuran trypanosomes, and their authors are named; another is an even more formidable list indicating the distribution of anuran trypanosomes by geographical regions and hosts; and the third is a list of Hirudinid vectors of anuran trypanosomes. Research on anuran trypanosomes was intensive during the first two decades of this century but then declined, to be revived only during the 1950s. In the sense that modern concepts of taxonomy, genetics, cytology, cell physiology and biochemistry have not yet been applied fully, the classification of anuran trypanosomes is still relatively undeveloped. The same is true of life cycles, reproductive patterns and polymorphism. A reliable classification is badly needed but to construct this is a difficult and even arbitrary task. However, a dynamic model of classification of anuran trypanosomes is proposed which can grow without needing regular total revisions. The phylogeny of the genus *Trypanosoma* can hardly be considered unless we can understand more fully the relationships between the trypanosomes of "higher" and "lower" vertebrates. The electron microscope has not yet been put to significant usage in this field, but we know that anuran trypanosomes are large and complex in structure, whereas mammalian trypanosomes are smaller and less complex, which may be examples of primitive complexity and secondary reduction of size and complexity. Study of the fine structure of anuran trypanosomes, may reveal much about the rather inscrutable structures of mammalian trypanosomes. Study of the

literature indicates that trypanosomes are ubiquitous in nearly all populations of Anura, perhaps denoting ancient origin. An effort has been made to integrate existing knowledge of anuran physiology and ecology, together with the ecology of the invertebrate host and trypanosome physiology and behaviour, into a dynamic model of host-parasite relationship. Another benefit of studying anuran trypanosomes will show in a broader context of pathogenicity. Possible endogenous adrenergic control systems have survived in the adaptation of mammalian trypanosomes to their homiothermic hosts. Leeches are regarded as the primary vector in anuran trypanosomiasis, but various insect vectors add further interest, underlining the important place occupied by anuran trypanosomes within the genus. Culture has been possible now for many years but generally only to provide experimental subjects for the study of nutrition, reproduction and metamorphosis. The writers hope that some effort in this area may be drawn away from the study of human trypanosomiasis with ultimate advantage.

Leonard J. Bruce-Chwatt deals with world problems of imported diseases. He shows that we must have knowledge of communicable disease if protective measures are to be established, and then states that the present international control established by W.H.O. has sufficed up to a point but that the enhanced amount and the heightened rapidity of international travel and trade has revealed danger of the spread of cholera, plague, smallpox, yellow fever and many other diseases of only slightly lesser importance. We must realise that tropical countries are not the only reservoirs of infectious diseases and that rapid urbanization and industrial development make for widespread redistribution of disease. The recognition of imported disease is now becoming the responsibility of medical practitioners, who must collaborate with higher authorities to protect travellers by means of vaccines, provide them with international certificates, advise on simple measures of protection whilst travelling abroad, and deal by diagnostic means with imported diseases when they return. Six major sections of this review have a rich content of information about the past and present of international health, international health regulations and increase of world air transport, the importation of animal diseases and vectors of disease, the major imported diseases, the common diseases of travellers, and prevention of imported disease by means of immunization. Major imported diseases include cholera, smallpox, yellow fever, plague and relapsing fever, and typhus. Common diseases of travellers include gastro-intestinal infections, malaria, trypanosomiasis, leishmaniasis, schistosomiasis, filariasis and other helminthiasis, rabies, arthropod-borne encephalitis, dengue, haemorrhagic fever, poliomyelitis and leprosy. One section is devoted to medical puzzles and diagnostic fallacies, which is highly significant because the commonest symptoms of disease may be present in a wide variety of infections. Some medical puzzles can be solved by means of simple, well-directed investigation, but many other cases may call for great circumspection. The traveller should become familiar with health problems and dangers when travelling abroad, and improvement of conditions must be continued and safety maintained by airline authorities, charter companies and travel agencies as well as by relevant health authorities.

William N. Beesley's very detailed review deals with methods and materials for the control of arthropods of medical and veterinary importance, which are sometimes parasites and just as often vectors of serious parasitic diseases. Control depends largely on the use of insecticides but good hygiene or animal husbandry is essential for its success. In the Introduction mention is made of benefits accruing from the use of insecticides: in malaria alone, eradication programmes may have saved more than 2000 million infections of the disease during a single recent decade. Difficulties are notable: more than 3000 species of mosquitoes exist; 350 species of *Anopheles* include 60 species that are known to be vectors of human malaria. Culicine mosquitoes include more than 500 species of *Aedes* and 300 species of *Culex*. *Aedes aegypti* is the vector of urban yellow fever, several types of dengue, virus and mosquito-borne haemorrhagic fever, and species of *Culex* transmit some types of arbovirus, encephalitis and filariasis. Most insecticides are synthetic chemicals (many of them with imponderable names: see the List on pp. 180-182) and they involve techniques of dusting, spraying or dipping, although other and more exotic means include the use of insect juvenile hormone, insectivorous fishes and viruses or fungi. Ten sections of this review trace out methods of arthropodan vector control: one deals with mosquitoes (anopheline and culicine), insecticide resistance, new insecticides and repellents, and genetic control; another section deals with blackflies and midges, and *Onchocerca* in animals; and other sections are concerned with domestic flies, tsetse flies, blowflies and screwworms, keds, oestrid flies, lice and fleas, and ticks and mites. There is also a section dealing with the future of arthropod control, summing up the situation existing after remarkable successes, but also indicating where further effort is required in the future. Epidemics of malaria, louse-borne typhus, plague, yellow fever and other diseases can flourish "despite all the paraphernalia of modern insect control programmes". Many millions of South Americans of all ages still suffer from Chagas' disease, many millions of Africans are victims of onchocerciasis and even more millions are victims of one or another form of filariasis. However, vast amounts of data are now available which bear on the distribution of pathogens and vectors on the face of the earth, greatly improved insecticides and methods of administration have led to hitherto unsuspected results. Micromethods in insect physiology linked with chromatographical analysis have indicated that minute amounts of some insecticides can affect insects at some or all stages of development. Insecticides resistance has been shown in the field of genetics to be due to single principal genes, and biological considerations are dependent on specialist laboratories of various kinds. In the future, we are told, vector control will for some time continue to depend on chemical insecticides, increasingly based on new types of chemicals, and there will be much more and closer integration of biological and chemical control techniques giving greater effect for least cost. Few vectors will be completely eradicated, but reduction of vector populations to minimal levels, with few parasites to transmit, will help to provide for a demanding and ever-increasing world population.

Kathleen M. Lyons has been concerned with the fine structure of the

"epidermis" and sense organs of some Turbellaria, Aspidogastrea and Monogenea. Following Donald L. Lee (vols 4 and 10 of this series of books) she has adopted the term "epidermis" for the outer covering of the body in Platyhelminthes, although some other writers have preferred "tegument" (see Hockley, pp 233-234) or "integument" for this living protoplasmic layer once commonly known as "cuticle" and wrongly regarded as a non-living, protective outer covering of the body. Turbellaria considered are members of the Acoela (e.g. *Convoluta*), Rhabdocoela (*Kronborgia* and *Syndesmis*), Temnocephalida (*Temnocephala*), Tricladida (*Dugesia*) and Polycladida (*Kaburakia*). Mention is made of two genera of Aspidogastrea (*Aspidogaster* and *Multicotyle*); the latter genus was considered in great detail by Klaus Rohde in vol. 10 of this series (1972). One major concern was the embryology and structure of the larval epidermis and the epidermis of adult Monogenea. The range of variability and of conformity in epidermal fine structure is considered in a number of monogenetic trematodes such as species of *Entobdella*, *Acanthocotyle*, *Rajonchocotyle* and *Polystoma*. In addition to regional differentiation, microvilli on the body surface of some Monogenea and the terminal webs of *Polystoma* and *Rajonchocotyle*, the secretory and lamellate inclusions of the "epidermis" and the plasma membrane and surface coat of adult Monogenea are considered, along with syncytial nature and surface differentiation. Finally, some general evolutionary considerations are made. The sense organs of Monogenea taken into consideration include eyes, organs ending in cilia, unciliate and compound multiciliate receptors. In final conclusion, there are indications of where in this field of study there is most promise of interesting results.

David J. Hockley's very detailed review of ultrastructure of the tegument of *Schistosoma mansoni* has four main sections, dealing respectively with the cercaria, the schistosomulum, the adult trematode and miracidium and sporocyst. The cercaria section concerns the development of the tegument, the cercarial surface coat and associated structures of the tegument in developed cercariae. A syncytial tegument connected to subtegumental cells occurs in all adult digenetic trematodes that have been examined and this unusual structure involves unusual cytoplasmic inclusions that are also related to the host-parasite interface. As schistosome cercariae penetrate the host directly, the tegument of the larva eventually becomes the tegument of the adult worm, not becoming involved in the formation of a metacercarial cyst as in *Fasciola hepatica*. The tegument of schistosomula is considered within 30 min to 3 h of penetration into the host and up to two weeks after penetration, after which this surface region is examined closely in adult worms, where sexual dimorphism necessitates noting differences in the tegument and associated structures in males and females, notably cytochemical differences. Specialized regions of tegument occur in the oesophagus and the uterus, which are regarded as tegumental structures but differ in structure. The oesophagus is primarily concerned with digestion, it is suggested, and the function of the intestinal caecum is absorption and egestion. Destruction of the tegument is specially considered in respect of the effects of hypo- and hypertonic media, drugs and host immunity. Finally, the epithelium and

associated structures of the miracidium are considered and the contrasting tegument of the daughter sporocyst, which has the syncytial tegument and nucleated subtegumental cells of the typical digenetic trematode. All these and other matters are considered in such intricate detail as is necessary at this time, when ultrastructural detail can improve our understanding of the host-parasite relationship in established schistosomiasis.

John D. Thomas's review is a contribution to our understanding of the epidemiology of schistosomiasis, a parasitic disease that has probably surpassed malaria in prevalence and continues to increase in some parts of the world despite expensive efforts to institute control measures. His review has four principal parts: a historical section deals with the rationale for focusing attention on the molluscan hosts, control of molluscs either by means of chemical molluscicides or by manipulation of environmental factors in various ways, and an alternative solution of parasite control by reducing the success of miracidia, sporocysts and cercariae, and of adult worms. The mathematical models that have been used to predict the probability of success of such possible control measures are said to lack precision and generality because certain facts are overlooked or wrongly interpreted, for instance, the immune response of the definitive host, the longevity of the adult parasite and parasite-induced mortality of the snail host, not overlooking the time-scale of various events. Here in this review are described the results of experiments designed to show how various environmental factors such as contacts resulting in copulatory behaviour, resources of food and ions in the external medium, and substances added to the medium either by snails or their plant food receive expression in growth and natality rates of individual snails (*Biomphalaria glabrata*; host of *Schistosoma mansoni*). Attention is given to the possibility that snails may produce specific inhibitory pherones and to other considerations, such as the effects of chemical conditioning and several effects were observed and are summarized in the final section of the review.

Jaroslav Šlais has produced a finely-detailed review on the functional morphology of cestode larvae, which show great variability during post-embryonic development. Following a brief Introduction there are seven sections and ultimate Conclusion. One section deals with the oncospherical stage and its development, i.e. formation of embryonic envelopes and the development of the penetration glands, the hooklets and their muscles. Then, in another section there is consideration of the structure of the oncosphere (hexacanth), its functional capability at the infective stage and subsequent metamorphosis. Other sections consider post-oncocercal development of larvae that do not form a cavity, e.g. the proceroid and plerocercoid of Pseudophyllidea and the larvae of Tetraphyllidea and Caryophyllaeidae, the tetrathyridium of *Mesocostoides* and larval stages of other genera, and similar stages of development of larvae which form a cavity, e.g. various cysticercoids, and the cysticercus. Special treatment is given to the functional morphology of the strobilar tegument of adult stages, histogenesis of the calcareous corpuscles and morphogenesis of the mature plerocercoid to the adult stage. The scolex of larval Taeniidae is examined in the cysticercoid and cysticercus, also the cyst wall of the cysticercoid and the cysticercus bladder. Excystment

of the cysticeroid and evagination of the cysticercus are noted. A sexual multiplication and abnormal growth are other topics dealt with. In conclusion we are told that successful cultivation of the oncosphere and other larval stages has produced much of this new information about the physiology of larval cestodes with the help of histochemistry and electron microscopy, information that facilitates more precise placing of these cestode parasites in the whole zoological system and improves our understanding of host-parasite relationships. Jaroslav Šlais believes that demonstration of the course of infection in the intermediate host, the establishment of the larva in its definitive host and the causes and forms of standard and abnormal growth of larval stages are perhaps the most significant advances made.

Reino S. Freeman points out that in the more recent systems of cestode classification there is wide disagreement on the limits, relationships and validity of various taxons, particularly at the level of orders. He doubts that there is even general agreement on six of the major orders, Tetrahyminthida, Tetraphyllida, Pseudophyllida, Protocephalida, Caryophyllaeida and Cyclophyllida. The systems are based mainly on adult morphology, especially scolex structure, and to a lesser extent on the uterus, position of the genital pores and the nature of the vitellaria but he places great emphasis on host specificity. For the most part these systems ignore cestode ontogeny, which has received little attention, and the need for taxonomic revision is now evident. Freeman discusses a basic cestode development cycle in an attempt to develop a unified system of naming the various stages of cestode development which suggests the course of evolution of cestode life cycles and may help to delineate the taxons in cestodes with a six-hooked larva, or oncosphere (hexacanth). The cestode life cycle is usually regarded as either two-host or three-host and rarely one-host, with a free-swimming stage only when in aquatic hosts, never in terrestrial hosts. Moreover, there is little agreement on the definition of the coracidium, proceroid, plerocercoid and cysticeroid forms. The review has four main sections between Introduction and Conclusions. One section deals with the basic cestode life cycle, its stages and ecology; another with variations in cestode ontogeny, the adult types of eggs and oncospheres. A section is then devoted to the evolution of life cycles and another to phylogenetic relationships. In conclusion, we are told that more data are required before a complete pattern of cestode ontogeny can emerge. This is true of early ontogeny and especially the origin, development and final disposition of the primary lacuna, cercoma, invaginal canal and excretory system of the metacestode. There is also a need for data bearing on growth patterns of metacestodes in the alimentary canals of vertebrates. However, data already available show that metacestodes follow recognizable patterns of growth, which may help to establish taxonomic relationships between cestodes.

John H. Rose tells us that although lungworms of sheep and pigs are less important and have been studied less intensively than other helminths of these hosts, they are being studied in many parts of the world and our knowledge of them has increased sufficiently in recent years to warrant this review. Four species of these nematodes infect pigs, namely *Metastrongylus elongatus*

and *M. pudendotectus*, which are cosmopolitan and have been well studied, and *M. salmi* and *M. madagascariensis*, which are little known. At least fourteen species of lungworms occur in sheep but only four of them are widely distributed and have been extensively studied: these are *Dictyocaulus filaria*, *Muellarius capillaris*, *Protostrongylus rufescens* and *Cystocaulus ocreatus*. The first three named species are cosmopolitan but *C. ocreatus* is restricted to parts of Europe, U.S.S.R., North Africa and the Middle East. The two main sections of the review deal with pig and sheep lungworms respectively and each of these sections is concerned with geographical distribution, incidence of infections, life cycle, pathology in the definitive host, immunity, treatment and control. Pig lungworms have been surveyed in pigs slaughtered at abattoirs and bacon factories and *M. elongatus* and *M. pudendotectus* occur, sometimes in almost equal numbers, although *M. elongatus* usually predominates. Incidence varies according to the age of pigs. The life cycle of these two species is similar; adult worms live in the bronchi and usually in secondary branches of the bronchioles. Eggs pass up the trachea, are swallowed and pass through the alimentary canal, to be thrown out in faeces. Pigs are infected by devouring earthworms of any one of a score of species which contain larvae derived from eggs swallowed. The life histories of sheep lungworms are treated separately and space does not permit mention here, except that individual land and freshwater molluscs serve as the intermediate hosts, a formidable list appearing in Rose's Table I. In considering treatment and control, only the more recently developed anthelmintics are referred to and control may depend on preventing pigs from ingesting infected earthworms and modifying methods of sheep husbandry, such as keeping sheep off pastures in the early morning and evening when the molluscan hosts are active.

The four short, updated reviews in this volume are concerned respectively with malaria in mammals excluding man, *Toxoplasma* and toxoplasmosis, the biology of the Acanthocephala, and the post-embryonic developmental stages of cestodes. Percy Cyril Claude Garnham's review on malaria has an introductory section and then sections dealing with taxonomic problems and new species, life cycles including exoerythrocytic and sporogonic stages, pathogenesis and culture, host susceptibilities and affinities, and fine structure. The most important discoveries of the last five years, we are told, are probably in the field of immunology, but dramatic research results concern the response of New World monkeys to the human species of *Plasmodium*. Taxonomic investigations leave unsettled the status of parasites beneath species level, but one major advance has been the use of isoenzyme analysis in the identification of species and subspecies in rodents. Numerical taxonomy is being pressed into service. Studies of ultrastructure are progressing and the use of scanning microscope techniques has given useful results, especially in relation to surface membranes after freeze-etching. Cytochemistry has not helped much in the determination of organelle functions but autoradiography may soon give useful clues. Two great problems that remain unsolved are the nature of anopheline susceptibility and resistance to various species of malaria, and the mechanism of relapses. These and other problems are discussed as fully as is possible.

Leon Jacobs's review (based on more than 200 from over 2,000 papers) deals with the life cycle and morphology of *Toxoplasma*, epidemiology, animal toxoplasmosis, human toxoplasmosis, serology and immunology, biology, chemotherapy, new knowledge of *Sarcocystis* and conclusions. The most important advance during the last six years is that much has been learned about the life cycle of *T. gondii*. However, other important studies have added to our knowledge of immune mechanisms in toxoplasmosis and how these relate to other intracellular infections and to tumours. In his previous review, Leon Jacobs cited instances in which transmission of *T. gondii* was obtained from cat's faeces which did not contain *Toxocara cati* eggs. This has stimulated other researchers interested in the contaminative route of infection of *Toxoplasma gondii*, and has led to the discovery that the nematode egg is not necessary in the life cycle of the protozoan. In this review research in some areas had to be neglected in favour of developments concerning the life cycle of the parasite and their implication in respect of epidemiology. In the future the balance may shift to immunology and the physiology and biochemistry of the parasite, hopefully to successes in chemotherapy and in the diagnosis of chronic disease.

Warwick L. Nicholas has given very full treatment of the biology of the Acanthocephala, indicating in his Introduction that interest in this group has increased and diversified since his previous review was written. One section of his updated review deals with morphology, functional anatomy and histology in respect of proboscis, trunk, uterine bell, acanthor and characteristic nuclei and nucleoli. In other sections there is consideration of development both in the intermediate and definitive hosts, fine structure of the tegument in adult and larva (acanthor), development and ultrastructure of spermatozoa, physiological matters including osmotic regulation and hatching of the acanthor, biochemical matters including intermediary metabolism, and host-parasite relationship. In a final section of the review there is a summary with conclusions. It is unnecessary in this place to go into details about all these topics, but readers will note that the nature of the "tegument" and its growth and development have been considered; other interesting topics are the mode of action of the uterine-bell apparatus and the movement of the acanthor. The relationship between Acanthocephala and Cestoda can now be better understood as a result of advances in knowledge of biochemistry and fine structure. Other comparisons between these two groups are made in relation to intermediary metabolism, and finally there is a phylogenetic explanation of peculiarities of acanthocephalan embryonic and larval development.

Marietta Voge's review on post-embryonic stages of cestodes has seven sections. Following the Introduction, one section deals with life cycles and larval growth in the orders Tetraphyllidea, Pseudophyllidea and Cyclophyllidea. The next section is concerned with histology, histochemistry and fine structure in Lecanicephalidea, Pseudophyllidea and Cyclophyllidea. Another section deals with host-parasite relationships in invertebrate hosts, vertebrate intermediate hosts and final hosts, with consideration of immunity. Finally, there are sections dealing respectively with metabolism and growth *in vitro*, followed by conclusions drawn. The author explains that recent trends

in research have shifted towards fine structure, metabolism and immunology, although life histories and morphological features have not been neglected. She has given many interesting developments, e.g. female hosts are more resistant to infection than male hosts, strain differences occur in *Taenia crassiceps*, and methods used can be useful for the detection of mutations. However, our ignorance of different (internal) environments available to the parasite in the host is great, likewise the composition of host body fluids (blood, serum) used in culture of parasites.

After completing my work on this book and at the beginning of a second decade of publishing *Advances in Parasitology* I am grateful to and thank friends and colleagues who have contributed to volume 11 of this series of books and who have thus helped to further my aim to organize and edit precious information and ideas that will assist progress in the modern biological field of parasitology. I am equally pleased to say thank you to other friends and colleagues on the staff of Academic Press for continued assistance in producing this book and thus helping what I regard as a worthy cause. It is a privilege to be able to continue production of this series of books, further volumes of which are assured.

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