THE BIOLOGY OF THE
COCCIDIA

Edited by

Peter L. Long, D.Sc., Ph.D.

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Preface

There have been a number of books on the coccidia, but few of them have been concerned with reviewing the full range of biological characteristics and host-parasite relationships. The late Dr. Datus M. Hammond, Dr. Erich Scholtyseck, and I thought that it was impossible for a single author to review the information adequately. Accordingly, in planning **The Coccidia: *Eimeria, Isospora, Toxoplasma, and Related Genera*** (Hammond, D. M., and Long, P. L. 1973), we enlisted the services of 10 scientists with special knowledge to write separate chapters on the taxonomy, biology, host-parasite relationships, pathology, pathogenicity and immunity, ultrastructure, in vitro culture, biochemistry, toxoplasmosis, and techniques. The present book includes similar subjects, except that there is neither a specialized chapter on *Toxoplasma,* so ably written by Dr. J. K. Frenkel in the previous book, nor a special chapter on techniques.

The coccidia are protozoa of the phylum Apicomplexa. Those belonging to the suborder Eimeriorina include the "true" coccidia and are the subject of the considerations of this volume. The coccidia cause coccidiosis, which is a disease of major economic importance in domestic animals. Parasites belonging to the genera *Eimeria, Isospora, Toxoplasma,* and *Sarcocystis* are discussed in depth, because these are the cause of disease and economic loss in animals. *Toxoplasma* is, in addition, an important parasite of man; *Sarcocystis* is potentially important. Information on *Toxoplasma, Sarcocystis,* and coccidia other than *Eimeria* are covered in each of the chapters, so that information on all of these interesting parasites may be discussed and compared.

Dr. Hammond and I soon realized that the exclusion of chapters on chemotherapy and control of coccidiosis from the previous book was a major error and, accordingly, chapters on these subjects are included in this volume. Also included is a chapter on "Genetics, Specific and Infraspecific Variation," because a great deal of information has been accumulated on this subject in the last few years. I am delighted that some of the authors who contributed to the previous book have written chapters in this volume. Also, I am pleased that Drs. L. P. Joyner, C. C. Wang, B. Chobotar, M. A. Fernando, T. K. Jeffers, L. R. McDougald, M. W. Shirley, H. D. Chapman, W. M. Reid, and R. Fayer have contributed to the present book.

In December, 1979, Dr. Erich Scholtyseck suffered a severe heart attack and was unable to complete the chapter alone. Dr. Bill Chobotar kindly agreed to help and by spending much time in Bonn in March, June, and July of 1980, completed Chapter 4.

Coccidiosis is an active area of research; several thousand scientific papers have been published on the subject. The aim of this book is to review the important advances that have been made in recent years. I am grateful for such a favorable response from the contributors who have set aside their research to write these reviews. My task has been made easier by the quality of their writing.

Each author was asked to discuss work published up to the end of 1979, although there are many references to work published in 1980. As in the last book, they were asked to discuss their own work and to interpret the work of others in their field of interest. We have tried to avoid repeating much of the information given in the 1973 book, but some discussion of that information is essential if useful reviews are to be achieved.

The classification and terminology used for the coccidia has been under constant review these past few years as new information has accumulated. There has been a great deal of controversy regarding this matter. However, the authors have used the terminology to which they are accustomed and have referred to published work exactly as it was cited. I have encouraged the contributors to avoid getting "bogged down" by these matters and they have responded by producing stimulating reviews. Perhaps my views on some of the taxonomy and terminology should be clarified. In dealing with generic and species names of parasites, I am sure that it is quite possible to use old names for parasites found today, and that, on the whole, fewer problems will arise by doing this. However, problems did arise in the terminology of some species of *Sarcocystis* when some authors used different species names in referring to the same parasite. With the objective of clarifying the situation, the names of the hosts were used as species names. It may seem useful to link the names of two hosts in the species name, but such a method is only valuable if a single species of *Sarcocystis* shares these hosts. The use of the name *S. bovicanis* has already lost much of its merit because two or possibly three bovine-canine species have been discovered.

Accordingly, I believe that the current international code of zoological nomenclature should be used and that the names *S. fusiformis* and *S. tenella* for the species *S. bovifelis* and *S. ovifelis*, respectively, are correct.

The generic name *Cystoisospora* has recently been used for parasites thought to differ from *Isospora* because sporozoites may have a dormant phase in a paratenic host. This might eventually be useful; however, at this stage more knowledge is required on the extent to which dormant stages occur in *Isospora* and other coccidia.

The book is intended for advanced undergraduates, graduate students, research workers, teachers with interests in both basic and applied aspects of the subject, and veterinary and medical scientists interested in the treatment and control of coccidiosis.

I am grateful to the authors for their cooperation throughout and to Dr. Levine for compiling a very useful glossary. I wish to acknowledge Geoffrey Mann, University Park Press, for his hard work, especially in the early stages, in helping me organize this new book and Loretta Cormier and Michael Treadway for their efforts in the production of this volume. Thanks are also due to Mrs. Jane Blount for the secretarial work. Finally, I wish to thank my wife, Verna, for helping me with the seemingly endless checking which was necessary.

Contents

1

Taxonomy and Life Cycles of Coccidia

Norman D. Levine

The history of our knowledge of the coccidia has been given by Levine (1973a, 1974), and will not be repeated here. The first coccidia were seen in 1674, when Leeuwenhoek found the oocysts of *Eimeria stiedai* in rabbit bile. However, they were not described until 1839 when Hake thought that they were a new form of pus globule. Lindemann (1865), who thought they were gregarines, named them *Monocystis stiedae*.

When it was recognized that the coccidia were protozoa, it was not realized that they had a complicated life cycle involving both sexual and asexual reproduction. As a consequence, the oocysts of the same species were placed in one genus (*Coccidium*) and the meronts (schizonts) in another (*Eimeria, Isospora,* etc.). The two stages were separated even more widely: Labbé (1899) put them in different suborders, and Minchin (1903) in different families. Stiles (1902) and Lühe (1902), whose view was eventually accepted, pointed out that they belonged to the *same genus and that the name Eimeria,* given by Schneider (1875), had precedence over the name *Coccidium,* given by Leuckart (1879). *Coccidium* is commemorated now only in the name of the groups to which *Eimeria* and its relatives belong and in the name of the disease that they cause. Books on the coccidia include Hammond and Long (1973) and Pellérdy (1974).

TAXONOMY

Coccidia are protozoa belonging to the phylum Apicomplexa and within it to the suborders Adeleorina and Eimeriorina. Some authors include all members of the subclass Coccidiasina; however, this definition is too broad. The suborder Eimeriorina, which comprises 10 families, 37 genera, and about 1,500 named species, includes the "true" coccidia, which are considered in this book. The diagnoses of the Apicomplexa, Eimeriorina, and related groups are given below, so that one can see how the true coccidia relate to the other groups and to each other. The diagnoses to suborder are those of the Committee on Systematics and Evolution of the Society of Protozoologists (Levine et al., 1980). The diagnoses of lower groups are those of this author. This classification is somewhat different from that given only a few years ago (Levine, 1973a). However, knowledge gained since then has necessitated the changes.

Phylum Apicomplexa Levine, 1970

Apical complex, generally consisting of polar ring(s), rhoptries, micronemes, conoid, and subpellicular microtubules, present at some stage; micropore(s) generally present at some stage; chilia absent; sexuality by syngamy; all species parasitic; about 4,000 named species.

Class Perkinsasida Levine, 1978

With flagellated zoospores (sporozoites?); zoospores with anterior vacuole; conoid forms

1

incomplete truncate cone; sexuality absent; homoxenous; about 1 named species.

Class Sporozoasida Leuckart, 1879

If present, conoid forms a complete truncate cone; reproduction generally both sexual and asexual; oocysts contain infective sporozoites which result from sporogony; locomotion by body flexion, gliding, undulation of longitudinal ridges or flagellar lashing; flagella present only in microgametes of some groups; pseudopods ordinarily absent, if present, used for feeding, not locomotion; homoxenous or heteroxenous; about 4,000 named species.

Subclass Gregarinasina Dufour, 1828

Mature gamonts extracellular, large; mucron or epimerite ordinarily present in mature organism, the mucron being formed from the conoid; syzygy of gamonts generally occurs; gametes generally similar (isogamous) or nearly so; similar numbers of male and female gametes produced by gamonts; zygotes form oocysts within gametocysts; life cycle characteristically consists of gametogony and sporogony; parasites of digestive tract or body cavity of invertebrates or lower chordates; generally homoxenous; about 1,430 named species.

Subclass Coccidiasina Leuckart, 1879

Gamonts ordinarily present; mature gamonts small, typically intracellular; conoid not modified into mucron or epimerite; syzygy generally absent but, if present, involves gametes; anisogamy marked; life cycle characteristically consists of merogony, gametogony, and sporogony; most species in vertebrates; about 2,420 named species.

Order Agamococcidiorida Levine, 1979

Merogony and gamonts both absent; in marine annelids; about 3 named species.

Order Protococcidiorida Kheisin, 1956

Merogony absent; in marine invertebrates; about 14 named species.

Order Eucoccidiorida Léger and Duboscq, 1910

Merogony present; in vertebrates and/or invertebrates; about 2,400 named species.

Suborder Adeleorina Léger, 1911

Macrogamete and microgamont usually associated in syzygy during development; microgamont produces 1 to 4 microgametes; sporozoites enclosed in envelope; endodyogeny absent; homoxenous or heteroxenous; about 440 named species.

Family Adeleidae Mesnil, 1903

Zygote inactive; sporocysts formed in oocysts; in epithelium of intestine and its appended organs, chiefly in invertebrates; about 40 named species.

Genus *Adelea* Schneider, 1875

Oocysts ellipsoidal or ovoid, with thin wall; oocysts with 6 to 48 flattened sporocysts, each with 2 sporozoites; in chilopods and mollusks; about 4 named species.

Genus *Adelina* Hesse, 1911

Oocysts spherical or subspherical, with thick wall; oocysts with 3 to about 20 spherical or ellipsoidal sporocysts, each with 2 sporozoites; in annelids, chilopods, and insects; about 17 named species.

Genus *Klossia* Schneider, 1875

Oocysts with quite numerous spherical sporocysts, each with 4 sporozoites; in mollusks and perhaps birds and mammals; about 9 named species.

Genus *Orcheobius* Schuberg and Kunze, 1906

Oocysts with 25 or more sporocysts, each with 4 sporozoites; in annelids; about 3 named species.

Genus *Chagasella* Machado, 1911

Oocysts with 3 sporocysts, each with 4 to 6 (or more) sporozoites; in intestine of insects; about 4 named species.

Genus *Ithania* Ludwig, 1947

Oocysts with 1 to 4 sporocysts, each with 9 to 33 sporozoites; in insects; about 1 named species.

Family Legerellidae Minchin, 1903

Zygote inactive; no sporocysts formed in oocysts; in diplopods, nematodes, or insects; about 6 named species.

Genus *Legerella* Mesnil, 1900

With the characters of the family; about 6 named species.

Family Haemogregarinidae Léger, 1911

Zygote active (ookinete), secreting a flexible membrane which is stretched during development; heteroxenous, life cycle involving 2 hosts, one vertebrate and the other invertebrate; merogony in various cells of vertebrates; gamonts in vertebrate blood cells; sporogony in invertebrates; gamonts with about 70 to 80 subpellicular microtubules; about 380 named species.

Family Klossiellidae Smith and Johnson, 1902

Zygote inactive; typical oocyst not formed; a number of sporocysts, each with many sporozoites, develops within a membrane that is perhaps laid down by the host cell; 2 to 4 nonflagellated microgametes formed by a microgamont; homoxenous, with gametogony and merogony in different locations in the same host; in kidney and other organs of host; about 12 named species.

Genus *Klossiella* Smith and Johnson, 1902

With the characters of the family; in mammals; about 12 named species.

Suborder Eimeriorina Léger, 1911

Macrogamete and microgamont develop independently; syzygy normally absent; microgamont typically produces many microgametes; zygote not motile;

1

sporozoites typically enclosed in a sporocyst; endodyogeny absent or present; homoxenous or heteroxenous; about 1,500 named species.

Family Spirocystidae Léger and Duboscq, 1915

Meronts vermicular, curved, with 1 end markedly narrowed; mature meronts coiled like a snail shell, with numerous nuclei; gametes dissimilar, nonflagellate; 1 oocyst per gametocyst; gametocysts and oocysts only in chlorogogen cells; oocysts very thick-walled, ovoid or piriform, with micropyle; each oocyst contains 1 coiled, vermicular naked sporozoite; about 1 named species.

Genus *Spirocystis* Léger and Duboscq, 1911

With the characters of the family; in oligochaetes; about 1 named species.

Family Selenococcidiidae Poche, 1913

Meronts develop as vermicules in host intestinal lumen; meronts with myonemes and a row of nuclei; about 1 named species.

Genus *Selenococcidium* Léger and Duboscq, 1910

With the characters of the family; in lobster; about 1 named species.

Family Dobellidae Ikeda, 1914

Male and female gamonts produced by micro- and macroschizogony, respectively; syzygy present; about 1 named species.

Genus *Dobellia* Ikeda, 1914

With the characters of the family; in sipunculids; about 1 named species.

Family Aggregatidae Labbé, 1899

Development in host cell proper; oocysts typically with many sporocysts; most genera heteroxenous, with merogony in one host and gametogony in another; syzygy absent; about 29 named species.

Genus *Aggregata* Frenzel, 1885

Oocysts large, with many sporocysts; sporocysts with 3 to 28 sporozoites; heteroxenous, with merogony in a decapod crustacean and gametogony in a cephalopod mollusk; about 17 named species.

Genus *Angeiocystis* Brasil, 1904

Oocysts with 4 sporocysts, each with about 16 sporozoites; gamonts at first in form of large sausage; possibly heteroxenous; known stages in polychaete; about 1 named species.

Genus *Merocystis* Dakin, 1911

Oocysts with many sporocysts, each with 1 sporozoite; merogony unknown; presumably heteroxenous; about 1 named species.

Genus *Pseudoklossia* Léger and Duboscq, 1915

Oocysts with no or many sporocysts, each with 2 sporozoites (if sporocysts occur); merogony unknown; presumably heteroxenous; known stages in mollusks; about 5 named species.

Genus *Grasseella* Tuzet and Ormières, 1960

Oocysts with many sporocysts, each with 2 sporozoites; in ascidians; about 1 named species.

Genus *Ovivora* Mackinnon and Ray, 1937

Oocysts with many sporocysts, each with up to 12 (?) sporozoites; homoxenous; in eggs of echiuroids; about 1 named species.

Genus *Selysina* Duboscq, 1917

Oocysts with no sporocysts but with a variable number of heliospores consisting of many sporozoites arranged in a circle around a residuum like the petals of a flower; in ascidians; about 3 named species.

Family Caryotrophidae Lühe, 1906

Oocysts without definite wall; sporocysts with 8 or 12 sporozoites; homoxenous; in polychaetes; about 2 named species.

Genus *Caryotropha* Siedlecki, 1902

Sporocysts with 12 sporozoites; about 1 named species.

Genus *Dorisiella* Ray, 1930

Sporocysts with 8 sporozoites; about 1 named species.

Family Cryptosporidiidae Léger, 1911

Development just under surface membrane of host cell or within its brush border and not in the cell proper; syzygy absent; oocysts and meronts with a knob-like attachment organelle at some point on their surface; oocysts without sporocysts, with 4 naked sporozoites; microgametes without flagella; homoxenous; about 10 named species.

Genus *Cryptosporidium* Tyzzer, 1907

With the characters of the family; in vertebrates; about 10 named species.

Family Pfeifferinellidae Grassé, 1953

Oocysts without sporocysts, with 8 naked sporozoites; fertilization of macrogamete through a vaginal tube; homoxenous; about 2 named species.

Genus *Pfeifferinella* von Wasielewski, 1904

With the characters of the family; in mollusks; about 2 named species.

Family Lankesterellidae Nöller, 1902

Development in host cell proper; syzygy absent; oocysts with or without sporocysts, but with 8 or more sporozoites; heteroxenous, with merogony, gametogony, and sporogony in the same vertebrate host; sporozoites in blood cells, transferred without developing by an invertebrate (mite, mosquito, or leech); infection by ingestion of invertebrate host; microgametes with 2 (?) flagella; about 30 named species.

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Genus *Lankesterella* Labbé, 1899

Oocysts produce 32 or more sporozoites; sporozoites with about 30 subpellicular microtubules; in amphibia; known invertebrate hosts leeches; about 4 named species.

Genus *Atoxoplasma* Garnham, 1950

Similar to *Lankesterella,* but in birds; sporozoites in leukocytes; known vectors are mites; about 17 named species.

Genus *Schellackia* Reichenow, 1919

Oocysts produce 8 sporozoites; in lizards; merogony in small intestine, connective tissue, and/or reticuloendothelial system; vectors are mites or Diptera; about 8 named species.

Family Eimeriidae Minchin, 1903

Development in host cell proper; without attachment organelle or vaginal tube; syzygy absent; oocysts with 0, 1, 2, 4, or more sporocysts, each with 1 or more sporozoites; homoxenous or at least without asexual multiplication in nondefinitive host; merogony within host, sporogony typically outside; microgametes with 2 or 3 flagella; without metrocytes, in vertebrates or invertebrates; about 1,340 named species.

Genus *Tyzzeria* Allen, 1936

Oocysts without sporocysts, with 8 naked sporozoites; in vertebrates; about 9 named species.

Genus *Eimeria* Schneider, 1875

Oocysts with 4 sporocysts, each with 2 sporozoites; in vertebrates and a few invertebrates; about 1,040 named species.

Genus *Mantonella* Vincent, 1936

Oocysts with 1 sporocyst containing 4 sporozoites; about 3 named species.

Genus *Cyclospora* Schneider, 1881

Oocysts with 2 sporocysts, each with 2 sporozoites; about 9 named species.

Genus *Caryospora* Léger, 1904

Oocysts with 1 sporocyst containing 8 sporozoites; about 22 named species.

Genus *Isospora* Schneider, 1881

Oocysts with 2 sporocysts, each with 4 sporozoites; usually in vertebrates; about 200 named species.

Genus *Diaspora* Léger, 1898

Oocysts unknown, sporocysts each with 1 sporozoite; sporocysts without bivalved wall, without longitudinal dehiscence suture; in invertebrates; about 1 named species.

Genus *Dorisa* Levine, 1979

Oocysts with variable number of sporocysts, each with 8 sporozoites; about 9 named species.

Genus *Wenyonella* Hoare, 1933

Oocysts with 4 sporocysts, each with 4 sporozoites; about 15 named species.

Genus *Octosporella* Ray and Ragavachari, 1942

Oocysts with 8 sporocysts, each with 2 sporozoites; about 2 named species.

Genus *Hoarella* Arcay de Peraza, 1963

Oocysts with 16 sporocysts, each with 2 sporozoites; about 1 named species.

Genus *Sivatoshella* Ray and Sarker, 1968

Oocysts with 2 sporocysts, each with 16 sporozoites; about 1 named species.

Genus *Pythonella* Ray and Das Gupta, 1937

Oocysts with 16 sporocysts, each with 4 sporozoites; about 2 named species.

Genus *Barrouxia* Schneider, 1885

Oocysts with many sporocysts, each with 1 sporozoite; sporocysts with bivalved wall, with a longitudinal dehiscence suture; about 10 named species.

Genus *Gousseffia* Levine and Ivens, 1980

Oocysts with 8 sporocysts, each with many sporozoites; about 1 named species.

Genus *Skrjabinella* Machul'skii, 1949

Oocysts with 16 sporocysts, each with 1 sporozoite; about 1 named species.

Family Sarcocystidae Poche, 1913

Heteroxenous, producing oocysts following syngamy; syzygy absent; oocysts with 2 sporocysts, each with 4 sporozoites, in intestine of a definitive host; with asexual stages in an intermediate host; about 105 named species.

Subfamily Sarcocystinae Poche, 1913

Obligatorily heteroxenous; asexual multiplication in intermediate (prey) host; last generation meronts (sarcocysts) in intermediate host form metrocytes, which give rise to bradyzoites, which are infectious for definitive (predator) host; oocysts sporulate in predator host tissues; sporulated sporocysts in its feces.

Genus *Sarcocystis* Lankester, 1882

Last generation meronts typically in striated muscles; merozoites elongate; about 90 named species.

Genus *Frenkelia* Biocca, 1978

Last generation meronts typically in central nervous system; merozoites elongate; about 2 named species.

Genus *Arthrocystis* Levine, Beamer, and Simon, 1970

Last generation meronts typically in striated muscle, jointed like bamboo; merozoites spherical; about 1 named species.

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Subfamily Toxoplasmatinae Biocca, 1956

Complete life cycle obligatorily heteroxenous, but asexual stages usually transmissible from 1 intermediate host to another; metrocytes not formed; oocysts do not sporulate in host tissues; about 14 named species.

Genus *Toxoplasma* Nicolle and Manceaux, 1908

Meronts in many types of cell; host cell nucleus outside meront wall; about 7 named species.

Genus *Besnoitia* Henry, 1913

Meronts in fibroblasts and probably other cells; host cell nuclei within meront wall; about 7 named species.

Suborder Haemospororina Danilewsky, 1885

Macrogamete and microgamont develop independently; conoid ordinarily absent; syzygy absent; microgamont produces about 8 flagellated microgametes; zygote motile (ookinete); sporozoites naked, with 3-membraned wall; endodyogeny absent; heteroxenous, with merogony in vertebrate host and sporogony in invertebrate; pigment (hemozoin) visible with the light microscope may or may not be formed from host cell hemoglobin; transmitted by blood-sucking insects; about 460 named species.

Subclass Piroplasmasina Levine, 1961

Piriform, round, rod-shaped or amoeboid, without conoid; without oocysts, spores, or pseudocysts; flagella absent; most genera without subpellicular microtubules; with polar ring and rhoptries; locomotion by body flexion, gliding or in sexual stages (in Babesiidae and Theileriidae, at least) by large axopodium-like "Strahlen"; asexual and probably sexual reproduction present; parasitic in erythrocytes and sometimes also in other circulating and fixed cells; heteroxenous, with merogony in vertebrate and sporozoitogony in invertebrate; sporozoites with 1-membraned wall; the vectors are thought to be ticks; about 150 named species.

The Apicomplexa include five principal groups of protozoa (gregarines, haemogregarines, coccidia, malaria parasites and their relatives, and piroplasms) plus a rather large number of transitional or dead-end groups or species. Only the coccidia, of which there are quite a few genera, are reviewed in this book. However, so little is known about many of the species that only the more important or common ones are discussed.

LIFE CYCLES OF SELECTED FAMILIES AND GENERA

The life cycles of the eucoccidia are quite similar. The basic life cycle is shown in Figure 1. The oocysts are ingested by a host animal, and the sporozoites are released from them. The sporozoites enter host cells, turn into meronts, and multiply by merogony, forming a variable number of merozoites by multiple fission. These enter new host cells, turn into meronts, and again multiply by merogony. There is ordinarily a small, fixed number of asexual generations. The last generation merozoites enter new host cells and become gamonts. Some (the macrogamonts) develop into macrogametes without further multiplication, while others (the microgamonts) divide asexually by multiple fission to form a large number of flagellated microgametes. Syngamy takes place to form a zygote; a wall is laid down around it, and it becomes an oocyst. The oocyst ordinarily passes out of the host and does not develop further (i.e., sporulate) until it reaches the outside. However, sporulation takes place within the host's body in *Sarcocystis* and *Frenkelia* (and also in some species of *Eimeria* and *Isospora* in fish and reptiles). Once the oocysts have left the body, the infection is over. Some immunity develops as a result of infection, but it is not usually so great as to prevent reinfection.

In some species of *Isospora,* a sporozoite may enter a lymph node or other cell of a host animal species in which it cannot mature, and grow into a giant sporozoite, which Markus (1978) has denominated a hypnozoite. Here it remains for weeks, months, or years and infects its natural host when the latter eats the foreign (transport) host.

There are three multiplications in the coccidian life cycle—merogony, gametogony, and sporogony. Coccidia are haploid throughout their life cycle, except in the zygote stage. The first sporogonous division is meiotic, reestablishing the haploid condition.

The life cycles of selected genera of coccidia are given below, some of which were discussed by Hammond (1973). Therefore, duplication of much of his material is avoided.

Adeleidae

Adelina cryptocerci Yarwood, 1937 lives in the intestine of the woodroach *Cryptocercus punctulatus.* Sporulated oocysts are ingested by the woodroach. Sporozoites are released in its intestine. They pass through the intestinal wall and enter the fatty tissues around the intestine, where they form meronts. These each produce 8 to 40 merozoites by the 25th day. Each merozoite enters a new fat-containing cell and forms an average of 16 to 32 new merozoites. Merogony may be repeated several times. The last generation merozoites enter new fat cells and become macrogametes or microgamonts. The microgamonts enter into syzygy with the macrogametes, and a thin gametocyst wall is secreted around them. The macrogamete and microgamont grow, and the latter produces four motile microgametes. One of these unites with the macrogamete, forming a zygote. A wall forms around the zygote, and its nucleus divides, first by meiosis and then by mitosis, to form 5 to 21 uninucleate sporoblasts. Each sporoblast lays down a wall around itself and becomes a sporocyst. Each sporocyst forms two sporozoites and a residuum within itself. The sporozoites invade new hosts (Yarwood, 1937).