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At the present time there are several opinions concerning the classifi-
cation of the Sporozoa. Doflein (1901, 1909), Poche (1913), Wenyon (1926),
Hartmann (1923), Yakimov (1931), Dogel' (1937), and others put the Sporozoa in
a separate class in the phylum Protozoa, while Calkins (1926), Hall (1953), and
Grassé (1953) make this group of parasitic protozoa a subphylum. Those authors
who consider the Sporozoa a class put a variety of forms in it. Leuckart (1879)
put only the gregarines and the coccidia in it. Schaudinn (1900) also included
some of the blood sporozoa and all of the cnidarian sporozoa (Myxosporidia,
Microsporidia, and Actinomyxidia)and even the Sarcosporidia. Hartmann (1907)
and Luhe (1913) first included the Haemosporidia in the Sporozoa, but later put
them in the group Binucleata along with the trypanosomes and other flagellates.
Doflein (1901), Kudo (1931), Dogel' (1937), and others put the Myxosporidia,
along with the Microsporidia and Actinomyxidia, in the Sporozoa. Poche (1931),
Luhe (1913), and Wenyon (1926) put the Myxosporidia in a separate class.

There is a difference of opinion about the content of this class
Sporozoa because its characteristics are not clearly defined. Up to now the
basis for dividing it into subclasses, orders, and suborders has been confusing.
For example, Doflein and Reichenow (1929), Hyman (1940), and Dogel' (1937, 1951)
put the Haemosporidia in a separate order and included in it the blood parasites
of the families Piroplasmidae and Theileriidae. Wenyon (1926), Doflein (1901,
1909), Doflein and Reichenow (1953), and others put the Haemosporidia in the
order Coccidia. Grassé (1953) excluded the Piroplasmidea from the Haemosporidia
and placed the latter as a suborder in the order Eimeriidea.

Those authors who accept one of these various classifications of the
Sporozoa usually do not question whether or not the relationships between the
separate, systematic groups united in one class are natural and show phylogenetic
connections. Some of these systems are highly artificial, uniting, solely on
the basis of a few immaterial characteristics, complex types of protozoa which
have very little in common. Strange as it may seem, such artificial systems
are very widespread. Very likely most authors of works on Protozoa and Inverte-
brate Zoology, both here and in foreign countries, accept one of these systems.
Therefore, it is necessary to examine the various classifications of the Sporozoa
in order to decide which is natural and congruent, and thus most correct.

Some groups of parasitic protozoa, included temporarily in the class Sporozoa, have been studied insufficiently. This greatly impedes conclusions about their systematic positions. These groups are Sarcosporidia, Haplosporidia, Piroplasmidea, and some members of Eimeriidea (Merocystis, Pseudoklossia, Myriospora, and others). Therefore, those statements which will be made below concerning these groups are not conclusive and can be changed upon receipt of new, factual data.

First we will examine the question about the content of the class Sporozoa. The majority of protozoologists believe that the Sporozoa are a class in the phylum Protozoa along with the other classes, Rhizopoda, Flagellata, and Infusoria. It is difficult to agree with Dobell and O'Connor (1921) who raised all these classes to phyla. This destroyed the phylogenetic principle of construction of a system. I doubt whether it is correct even to make the Sporozoa a subphylum as Calkins (1933), Grassé (1953), and others do. Grassé artificially raised two similar groups - gregarines and coccidia - to classes, thus breaking their phylogenetic unity and causing the Sporozoa to lose its solidity.

Leuckart originated the class Sporozoa in 1879 and put the gregarines and coccidia in it. In 1900 Schaudinn added the Haemosporidia and Cnidosporidia and divided the class into two subclasses, Telosporidia and Neosporidia. The first subclass is characterized by sporulation terminating its life cycle, and by the absence of polar filaments in the spores. In the second subclass the spores develop thruout the life cycle and possess polar filaments. In the first subclass Schaudinn included gregarines, coccidia, and haemogregarines. In the second subclass he put Myxosporidia, Microsporidia, Actinomyxidia, Sarcosporidia, and Haplosporidia. Hartmann (1923) put the Sarcosporidia and Haplosporidia in another subclass, Acnidosporidia. Kudo (1931), Dogel' (1937), and others agreed with Hartmann, but Doflein and Reichenow (1929) considered each of these groups an independent subclass. So little is known about the Sarcosporidia and Haplosporidia that it is impossible at this time to come to a conclusion about their systematic positions. Wenyon correctly placed these "sporozoa" in a group of protozoa of vague systematic position.

Schaudinn's system was widely accepted by protozoologists and became firmly established in all the text books. However, the union of Telosporidia and Neosporidia in one class is artificial and has no factual basis, according to detailed analyses of structure and growth of their members. It is possible to say this even though the life cycle of the Neosporidia has not been thoroughly studied. Hartmann (1907) noticed the difference between the two subclasses and suggested that the class Sporozoa be divided into two independent classes, Telosporidia and Neosporidia, since they have a different plan of structure and different origins. The first group comes from flagellates and the second from Sarcodina. Wenyon (1926), Yakimov (1931), Epshtein (1931), and others agreed with Hartmann.

In Schaudinn's concept, the class Sporozoa is characterized by its life cycle. Spores are formed by multiple division and covered with a special membrane. As a result of the latter the parasites are isolated. The spore is formed by sexual reproduction and corresponds to the stage of a zygote. All the sporozoa are parasites. They do not have contractile and food vacuoles; therefore, the principal unifying characteristic is the spore. However, the spores of Telosporidia and Neosporidia are quite different in structure and origin. Since there is more than one definition of "spore", forms which are not homologous are recognized under this term.

The spores of the gregarines are called encysted zygotes. By means of multiple division of the zygotes, sporozoites are formed in the spores. In the coccidia the spores are called the encysted product of zygote division, and formed under the protective membrane of the zygote (oocyst), The zygote divides into two, four, eight or many sporoblasts. After a thick membrane is deposited on their surface, they are called sporocysts (or spores); sporozoites are formed in the sporocysts. The formation of the sporocyst wall in addition to the oocyst wall guarantees the best survival of the sporozoites in the external environment.

The spores of the gregarines develop differently from those of the coccidia, and these spores or encysted zygotes correspond to the coccidian oocysts. In the gregarines, the oocyst wall appears only after gametic syngamy and formation of the zygotes. The gregarines do not have the preparatory process of wall formation in the macrogamete that the majority of the coccidia do, nor do they have the typical oogamy peculiar to the latter. Among the coccidia, for example, in the Haemosporidia, the oocyst wall forms after the formation of the zygote; but in the majority, plastic material accumulates in the macrogametes, and after fertilization the cocyst wall forms from this material. The name "oocyst" emphasizes only that after fertilization the wall of the zygote forms at the expense of material already existing in the wall of the macrogamete.

If the "spore" of the gregarines and "oocyst" of the coccidia refer to the same stage of the cycle, namely, the encysted zygote (zygotecyst or cystozygote, according to Dogel', 1951); then it would be more correct to use the same term in all the groups of the Sporozoa. In his book, Wenyon (1926) called the spore of the gregarines oocysts; however, in the etymological sense he is not correct because the gregarines do not have typical oogamy. It is possible to disregard this fact because essentially the term "oocyst" means "zygotecyst", independent of mode and time of wall formation. In spite of the differences in the fertilization process (oogamy in the coccidia and isogamy, anisogamy in the gregarines), the encysted zygotes (zygotecyst) are homologous and analogous in formation. It is not correct to call the encysted zygote a spore because spores are formed within the oocysts of the coccidia, and these spores (as it was pointed out earlier) do not correspond in origin to the oocysts of the gregarines. The use of spore would include different formations and create additional difficulties in terminology. It is more correct to retain the term "oocyst" for the zygocyst of the gregarines and coccidia. Therefore, in general the gregarines do not have spores, and the same is also true of some of the coccidia (Cryptosporidia, Lankesterella, Dobellia, and others). In the oocysts of all the Telosporidia, the sporozoites are the final stage of sporogony.

Now we will compare the oocysts and spores of Telosporidia with the spores of Neosporidia. The spores of Neosporidia form in pansporoblasts and have one or several polar filaments. Doflein (1901) called this group Cnidosporidia, contrasting it with the other sporozoa in which the polar filaments were absent. The multi-cellularity seems to be an essential difference in the spores of the Cnidosporidia. For example, in the Myxosporidia two nuclei of the sporoblasts participate in the formation of the spore wall. Also a pair of nuclei participate in the formation of the polar filaments, and finally an ameboid embryo or sporoplasm with two nuclei develops in the spore. Nothing similar to this is observed in the Telosporidia.

Do the spores of Cnidosporidia compare with the oocysts or spores of Telosporidia as to origin? This question is difficult to answer. The life cycles of many members of Cnidosporidia have been poorly studied, and the concept of the same cycle differs among investigators. Little is known about the position of the fertilization process in the life cycle and the origin of the spores. I have not investigated this problem in detail so I will mention only that Naville's (1928, 1930) opinion about the life cycle of Myxosporidia is very doubtful. The presence in the cycle of two alternating fertilization processes, with two zygotes and two reduction division processes, is very improbable. The investigations of Noble (1941, 1943, 1944), concerning the life cycles of Cera-tomyxa and Myxidium are more likely. Noble believes that the nuclei of the sporoplasm are gametes (isogametes!), which fuse after the spore forms. Thus the sporoplasm with synkaryon is already a zygote, and when it enters a new host it first produces a trophozoite (a growing vegetative individual).

If, according to Naville, the pansporoblast forms from a zygote, which was produced by fusion of the gametes within a growing trophozoite, then Noble believes that the pansporoblast, containing spores, was produced by agamous rather than sexual reproduction, and actually preceded the formation of the zygote. From Noble's observation, the pansporoblast and the spore of Cnidosporidia do not correspond in origin to the oocyst or spore of Telosporidia, and they represent unique formations not comparable to any in the Telosporidia. In the Telosporidia the appearance of the oocyst as an encysted zygote completes the sexual process, and the spores develop by the metagamous process inside the oocyst. In the Cnidosporidia the spores precede the formation of the zygote, and fusion of the nuclei of the gametes occurs inside the spore, or even after the spore enters a new host and as the binucleated embryo is leaving the spore (Ceratomyxa). Thus, the Cnidosporidia has a brief sexual process which occurs inside the spore; whereas the Telosporidia has a well-developed sexual process which precedes the formation of the oocysts and spores.

The spores of the Cnidosporidia and the oocysts of the majority of the Telosporidia spread the parasites. After the spore of the Cnidosporidia enters a new host and the amoeboid embryo leaves it, the embryo becomes a diploid zygote (after fusion of the nuclei of the gametes) and develops into a trophozoite. After the oocyst of the Telosporidia enters a new host, uninucleated, vermicular sporozoites (the majority haploid) are released and become agamonts or gamonts. In the Cnidosporidia there are no stages which correspond to sporozoites, since the zygote in the spore does not undergo metagamous division, as is observed in the Telosporidia during sporogony.

In the Cnidosporidia the metagamous process occurs when the spore, containing sporoplasm, enters the host. However, this process cannot be compared with that of Telosporidia since they form quite different states. In the one case, sporozoites are formed inside the oocysts. In the other case, multi-nucleated trophozoites are formed in which pansporoblasts with spores develop. In some of the Myxosporidia (Ceratomyxa, Noble, 1941) the zygote directly gives rise to pansporoblasts; otherwise it is not essentially different from other Cnidosporidia.

The above data on the structure and origin of the spores of the Cnidosporidia and Telosporidia are sufficient to permit discussion of the principal differences between the subclasses. The entire life cycle of the Cnidosporidia differs sharply from that of the Telosporidia. First of all, the Cnidosporidia

do not have alternation of generations and a prominent sexual process with characteristic gametogenesis. The process of asexual reproduction is different in the Cnidosporidia than in the Telosporidia. In the latter, schizogony takes place; merozoites are formed and produce new generations of agamonts or gamonts. In the Cnidosporidia there is no true schizogony (Noble, 1944), although many authors use this term for the designation of asexual reproduction. In the Myxosporidia there is a multi-nucleated stage produced by the multiple division of the nucleus of the growing trophozoite. Simultaneously portions of the protoplasm, each with a nucleus, break apart. Some of these uninucleated forms become pansporoblasts. This kind of reproduction is not schizogony. There is no recurrence as in schizogony of Telosporidia, and new generations of agamonts are not formed. Sometimes plasmotomy or budding of the trophozoite occurs. The term "nucleogony" was suggested by Noble for the process of producing a multi-nucleated trophozoite from a uninucleated one. Finally, in the majority of the Telosporidia all the stages of the life cycle, except the zygote, are haploid, since the first metagamous division is reduction. Mulsow (1911), Calkins and Bowling (1926), and Naville (1927) mentioned gametic reduction only in a few monocystids. However, Wenyon (1926) and Doflein and Reichenow (1953) stated that these observations should be regarded with caution, since the authors had a mixed infection of worms with several species of monocystids (with various numbers of chromosomes); therefore ,they could have easily arrived at a mistaken conclusion. Naville (1930) believes that the Myxosporidia have two haploid phases: the gametes of the plasmodium (extremely doubtful!), and the two nuclei of the sporoplasm (dihaplophase) in the spores. On the other hand, Noble (1941, 1944) definitely believes that all stages in the life cycle of the Cnidosporidia are diploid and only the nuclei of the sporoplasm are haploid,. since reduction division results in their formation into a spore.

Many characteristics of Telosporidia, such as diflagellated microgametes, the structure of the merozoites, the character of the sexual process, and others suggest that they originated from flagellates. The Cnidosporidia in no way resemble the flagellates, but they are similar to the Rhizopoda (Hartmann, 1907) in the structure of the amoeboid plasmodium and the primitiveness of the sexual process (autogamy).

Therefore, the differences between the Cnidosporidia and the Telosporidia are so considerable that these groups should be in separate classes. Hartmann's (1907) suggestion that Telosporidia and Neosporidia be recognized as separate classes should have been accepted a long time ago. It would not be correct to abolish the term "Sporozoa". Hartmann made this mistake, but corrected it later (Hartmann, 1923). He substituted the class name "Telosporidia" with Leuckart's term "Sporozoa", and enlarged the class by including the Haemosporidia in it. This system, with some alterations, was adopted by Wenyon (1926) and then by Yakimov (1931). Doflein (1901) changed the name of the class Neosporidia to Cnidosporidia on the basis of the structure of the spore.

First, we will try to give the characteristics of the class Sporozoa. All the sporozoa are intracellular or extracellular parasites of vertebrates and invertebrates. The life cycle consists of alteration of sporogony and the sexual process or alteration of recurring agamous generations, the sexual process, and sporogony. The type of asexual reproduction is schizogony. Gametogenesis takes place in the progamous period, and is either similar in both sexes (gregarines) or dissimilar (coccidia). As a result of isogamy, anisogamy, or oogamy, a zygote is formed which encysts and becomes an oocyst (zygocyst).

Sporogony takes place in the oocyst, and a varied number of vermicular sporozoites is formed. The sporozoites (infective stage), upon entering a suitable host, develop into agamonts or gamonts.

The systematic position of the Haemosporidia could not be determined, even though Danilevskiĭ (1885) wanted to include them in the class Sporozoa. Bütschli (1887), Labbé (1896), Delage and Hérouard (1898), Doflein (1901, 1909), Poche (1913), and a number of others supported this point of view. However, they put quite different groups in the Haemosporidia. For example, Danilevskiĭ (1886, 1888) included Hemocytozoa (a gregarine of turtles), Hemocytozoa (of birds) which are Haemoproteus, and the malarial plasmodia. Minchin (1903) put in the genera Plasmodium, Haemoproteus, Babesia, Lankesterella, Haemogregarina, and Hepatozoon. Doflein (1909), in addition, included Karyolysus, Leucocytozoon and Leishmania (!). Poche (1913) put Halteridium (Haemoproteus), Leucocytozoon, Babesia, and Plasmodium in a suborder of Haemosporidia.

On the other hand, Hartmann (1907), Hartmann and Jollos (1910), Léger and Duboscq (1910), and Lühe (1913) united all the Haemosporidia with the trypanosomes in the order Binucleata, placing them in the class Flagellata. They did this on the mistaken observations of Schaudinn (1904), thinking, for example, that the Haemoproteus were intracellular stages of trypanosomes (T. noctuae). The process of flagellation in the Haemosporidia and the discovery of flagella in Babesia served as important arguments for including these organisms in the class of the flagellates. Meanwhile, further investigations showed this opinion of Hartmann and others to be without foundation, which strengthened the position of the Haemosporidia in the Sporozoa. The studies of the life cycles of the Haemosporidia brought to light the heterogeneity of the group. Some of the blood sporozoa were put in the group Adeleidea, and others were included in the independent group Haemosporidia with the genera (Plasmodium, Haemoproteus, and Leucocytozoon.

Minchin (1912), Hartmann (1923), Doflein and Reichenow (1929), Dogel' (1927, 1951), Boyd (1949), Hoare (1949), and others considered Haemosporidia an independent order equivalent to the gregarines and coccidia. Hall (1953) raised the Haemosporidia, Gregarinida, and Coccidia to subclasses. The genetic connection among all these groups of Sporozoa was broken by this change.

On the other hand, the opinion for a long time has been that the Haemosporidia should be united with the coccidia. Mechnikov (1886) correctly expressed the idea that "the microorganism of malaria most probably should be placed in the group of coccidia..." Doflein (1901), on the basis of the resemblance of their sexual processes, united Haemosporidia and the coccidia in one order - Coccidiomorpha, on a par with the other order - Gregarinida. A few investigators developed this correct idea of uniting the Haemosporidia and the coccidia. Doflein continued his system in his own book on Protozoology through four editions (to 1916). However, in the fifth edition (1929), which was with Reichenow, the order Coccidiomorpha disappeared, and Haemosporidia was considered a separate order equal to the coccidia. Finally, in the sixth edition (1953) of this text, Reichenow named Haemosporidia a suborder in the order Coccidia, corresponding to the Coccidiomorpha of Doflein.

Those authors who put Haemosporidia in a separate order distinguished it from the coccidia (Adelidea plus Coccidia) on the basis of the following characteristics: The Haemosporidia parasitize the blood cells, but the coccidia

generally are found in the epithelial cells of internal organs. The sporozoites are formed naked in the oocyst in the Haemosporidia, while they occur in spores in the coccidia. In the former, the zygote is motile and the oocyst grows during sporogony; in the latter, the zygote is immobile and does not increase in size. However, these differences are not so great as to contrast Haemosporidia with the coccidia. Among the latter, there are some members whose sporozoites localize in erythrocytes and whose schizonts appear in the intestinal epithelium (Schellackia). The gamonts of the Haemogregarines (from Adeleidea) are found in the erythrocytes, but other stages of the cycle are found in the endothelium and other cells of internal organs. On the other hand, in the Haemosporidia not all stages of development in the vertebrate host occur in the blood cells. Schizonts, for example, develop in the reticulo-endothelial and hepatic cells. The absence of spores in the oocyts of Haemosporidia does not distinguish this group from the coccidia because, among the latter, Cryptosporidium, Pfeifferinella, Lankesterella, Schellackia, Tyzzeria, and Dobellia do not develop spores in their oocysts. A motile zygote (ookinete), is found in the coccidia in the genus Hepatozoon, and an oocyst which increases in size is present in Karyolysus.

At the same time, the Haemosporidia and the coccidia have a number of important characteristics in common which distinguish them from the gregarines. The coccidia (Adeleida, Eimeriidea) and the Haemosporidia are alike, as Doflein correctly observed, in the fact that both have male and female gametes which differ sharply from one another, and oogamy always takes place in both. Gametogenesis, which occurs differently in the male and female gamonts, is similar in the two groups. Two to four to many thousands of microgametes are formed from one microgamont. Microgametes usually have two flagella or are themselves filiform. On the other hand, with the completion of progamous division, the macrogamont becomes only a single macrogamete and is considerably larger than the microgamete. Asexual reproduction is carried out by means of schizogony. Several generations of schizonts are produced and develop intracellularly.

The Haemosporidia and Coccidia can be united in one group on the basis of these general, but essential, characteristics. Wenyon (1926) correctly called this group the subclass Coccidiomorpha and distinguished it from another subclass Gregarinina (or Gregarinomorpha according to Grassé, 1953). In the latter subclass the male and female gamonts form gametes which are similar in structure; in the case of Ophryocystis, large numbers of gametes are produced. They are formed by multiple division on the surface of the gamonts, and isogamy or different degrees of anisogamy takes place. Male gametes are monoflagellated. Pairs of gamonts unite in syzygy; a membrane surrounds them and they are called gamontocysts. The gamonts are located intracellularly only during the earliest stage of development; later, they convert to extracellular parasitism as trophozoites or vegetative forms. Schizogony occurs only in the schizogregarine, but the remaining characteristics are typical for this subclass. In contrast to the Coccidiomorpha, the gregarines parasitize only the invertebrates. We will not discuss the Gregarinina further since there are no contradictory opinions concerning it.

We will examine now the interrelation of the individuals which make up the subclass Coccidiomorpha. Doflein (1901, 1902, 1909) called the Coccidiomorpha an order and divided it into two suborders, Coccidia and Haemosporidia, and in the latter included Leishmania. The contents of these suborders do not correspond with the present data, and some of their members belong to a separate group, Adeleidea. Poche (1913) called this subclass the order Eimeriidea and divided it into three suborders, Selenococcidiinea, Eimeriinea, and Haemosporidia;

in the Eimeriinea he included the Adeleidea. Wenyon (1926) and Calkins (1933) considered the Coccidiomorpha a subclass and divided it into two orders, Adeleida and Coccidiidea. Wenyon divided the Coccidiidea into two suborders, Eimeriidea and Haemosporidiidea; and Calkins added a third, Babesiina.

Doflein and Reichenow (1953) called this group the order Coccidia, which corresponds in content to Wenyon's subclass Coccidiomorpha, and divided it into three suborders - Adeleidea, Eimeriidea, and Haemosporidia. Earlier (1929) these authors did not include Haemosporidia in the order Coccidia.

Grassé (1953) raised the Coccidiomorpha to a class and divided it into two subclasses: Prococcidia Léger and Duboscq, 1910, with one member, Seleno-coccidium; and Eucoccidia Léger and Duboscq, 1910, with the remaining members of Coccidiomorpha. He divided the Eucoccidia into two orders, Adeleidea and Eimeriidea. There is no good reason to put Selenococcidium in a separate sub-class or order (as Léger and Duboscq, 1910, did). Although this genus forms vermicular schizonts and gamonts extracellularly, it eventually enters the epithelial cells, and its sexual process is the same as in the members of the Eimeriidea. That is, a large number of flagellated microgametes are formed on the surface of the microgamont. Therefore, it is not correct to contrast Seleno-coccidium with the other coccidia as Grassé did, for such a system is artificial. More correct and natural is the division of the Coccidiomorpha into the orders Adeleida and Coccidiida (Wenyon).

In 1953 Grell described a coccidium from the body cavity of Dinophilus and unfortunately named it Eucoccidium dinophili. Schizogony is absent and the gamonts develop extracellularly in the body cavity of the worm. It is not a typical coccidium and the name Eucoccidium does not fit. It resembles the gre-garines but, since the male and female gametes are dissimilar, it belongs in the subclass Coccidiomorpha. Grell believes that the coccidia should be divided into Eucoccidia and Schizococcidia; however, he did not define the taxonomic units. Since schizogony and extracellular growth of gamonts and gametes are absent, and since the life cycle is comparatively simple, it is possible to place this coccidium in a special order on an equal basis with Adelieda and Coccidiida and call it Protococcidia. In some invertebrate coccidia (Angeiocystis, Myriospora, Merocystis, and others), the sexual stages have been described, but schizogony has not been observed. Probably they have no schizogony and develop like Eucoccidium (Grell, 1953). In this case, all these coccidia should be placed in the new order Protococcidia. On the other hand, Wenyon (1926) and Bhatia (1933) stated that, by analogy with Aggregata, schizogony of these coccidia takes place in other hosts which are still not known. Thus, they should be included, as is Aggregata, in the order Coccidiida.

The orders Adeleida and Coccidiida differ from Protococcidia. Schizogony is present and the gamonts develop intracellularly. In the Adeleida, the micro-gamonts and macrogamonts develop in contact with one another. Only 2 to 4 micro-gametes are formed from one microgamont (which is smaller than the macrogamont). The gamonts are infrequently surrounded with a common membrane like the gamonto-cysts of the gregarines; however, those of the adeleids develop intracellularly. In the order Coccidiida, the macro- and microgamonts develop separately. In those coccidia whose gametes form intracellularly, a large number of flagellated microgametes develop on the surface of the microgamont. In those coccidia whose gametes form in the intestinal lumen of the invertebrate host, the microgamont produces from six to 10-12 flagellated and long microgametes.

It is not quite clear in which of the orders to put <u>Dobellia</u> <u>binucleata</u> Ikeda, 1914, which parasitizes the intestinal epithelium of the sipunculids. Wenyon (1926), Grassé (1953), and others put this genus in the Adeleida because the microgamont develops in contact with the macrogamete. Doflein and Reichenow (1929, 1953) believe that it is a representative of the Coccidia, since a large number of microgametes are formed. I agree with the latter authors, and I believe that true syzygy does not take place in <u>Dobellia</u> as it does in many Adeleida. The development of gamonts together in a single host cell is seen even in the typical Eimeriidea (Cheissin, 1940, 1947); it is a secondary phenomenon and the same is true in <u>Dobellia</u>. The primary characteristic of this genus is the large number of microgametes produced. In the Adeleida, the primary features of development are the small number of microgametes formed, syzygy, and intracellular location of the gamonts.

Two families, Adeleidae and Haemogregarinidae, are included in the order Adeleida. In the life cycle of the Haemogregarinidae there is alternation of hosts and infection of the blood cells in the vertebrate host.

Various authors do not agree on the content of the order Coccidiida. It is natural to divide this order into the suborders Eimeriidea and Haemosporidia, and this scheme was accepted by Wenyon (1926) and Yakimov (1931). Bütschli (1882), Léger and Duboscq (1910),Calkins (1912, 1926), Doflein (1901, 1909) and a number of other authors put the adeleids in the order (or suborder) Coccidia, but without the haemogregarines, and excluded the representatives of the suborder Haemosporidiida. Léger (1911), Poche (1913), Hartmann (1923), Doflein and Reichenow (1929), Dogel' (1937), Kudo (1931, 1946), Hoare (1949), and many others included in the order Coccidia all the adeleids and eimeriids, but excluded the Haemosporidia. Hall (1953) made the Coccidia a subclass and included only the Adeleida and Eimeriida (without the Haemosporidia). According to Grassé (1953), the order Coccidiida corresponds to the order Eimeriidea plus the subclass Prococcidia with the one genus <u>Selenococcidium</u>.

It is justifiable to include the Haemosporidia in the order Coccidia because of the similarity of its sexual cycle with that of the suborder Eimeriidea. However, there are differences in these cycles. In the Eimeriidea, the flagellated microgametes form intracellularly in large numbers on the surface of the microgamont; whereas, in the Haemosporidia, flagellum-shaped gametes are produced in small numbers extracellularly in the intestinal lumen of the vector. Location, intracellularly or extracellularly, is a determining factor in the morphology and numbers of microgametes produced. In the Eimeriidea, the zygote is intracellular and consequently immobile; the oocyst, possessing a thick membrane, does not increase in size during sporulation. In the Haemosporidia, the zygote develops in the intestinal lumen of the host and is motile (ookinete); the oocyst, which lies inside the body of the host, is surrounded by a thin membrane and increases considerably in size during sporogony.

The majority of the Eimeriida complete their life cycle in one host. In the Haemosporidia, agamous reproduction and gamont formation occur in the vertebrate host, and gametogenesis and sporogony take place in the invertebrate host. In the Haemosporidia, the gamonts, sometimes the schizonts, localize in the erythrocytes; whereas in the Eimeriidea, development takes place in the epithelial cells of various organs. Only in two species do the sporozoites penetrate the erythrocytes.

The classification of the suborder Eimeriidae has not been definitely decided because there is a difference of opinion about the division of suborders into families. Lühe, Reichenow, and Wenyon divide this suborder into five to six families, based on the characteristics of the endogenous stages. Other authors base their classifications on the morphology of the ripe oocysts. Schneider (1881), Bütschli (1882), Labbé (1899), Minchin (1903), and others classify the coccidia according to the number of spores in the oocyst. For example, Minchin (1903) and Doflein (1909) divide all coccidia into four families: Asporocystidae, Disporo-cystidae, Tetrasporocystidae, and Polysporocystidae. Léger (1900, 1911), Poche (1913), and others, on the basis of the number of sporozoites in the oocyst, divide the Eimeriidea into three subfamilies: Tetrazoic, Octozoic, and Polyzoic. These above families differ also according to the number of spores in the oocysts; and, based on this fact, Léger (1911) lists eight families. Hoare (1933), Bhatia (1938), and others leave only two families, Selenococcidiidae and Eimeriidae, in the suborder Eimeriidea, which differ according to their life cycles. Grassé (1953) places each genus in a separate family, and according to his system, the suborder Holoeimeriidea divides into 20 families, differing in the structure of the ripe oocysts.

Undoubtedly, the division of the suborder into families should be based on the characteristics of the life cycle of the parasite and not on the structure of the ripe oocyst. This latter characteristic can serve as a criterion only in relation to the subfamilies and genera and, in a number of cases, species.

I do not believe it is possible to consider Hoare's classification correct, since it includes in the Eimeriidae different forms, such as Aggregata and Schellackia, which possess specific peculiarities in their life cycles. Further-more, it is wrong to create many families (Grassé) that differ only in the struc-ture of the ripe oocysts, thereby ignoring the similarities in the endogenous stages.

The members of Eimeriidae characteristically develop in one host, and their oocysts are excreted into the external environment. Probably, upon further investigation of Dobellia, this genus will be placed in the above family because its life cycle is not essentially different from that of the Eimeriidae. I con-sider the family Lankesterellidae equal with the above family. Its members develop alternately in vertebrate and invertebrate hosts. The oocysts are not excreted into the external environment, but the sporozoites invade the erythro-cytes and subsequently enter the vector.

In the life cycle of the family Aggregatidae, two invertebrate hosts are involved, and the oocysts are excreted into the external environment.

Finally, the family Selenococcidiidae should be included in the suborder Eimeriidea. It has vermicular, extracellular schizonts and gamonts, and develops in one host.

Wenyon's (1926) families, Cryptosporidiidae and Caryotrophidae, are not suitable because their life cycles are not different from those of the other Eimeriidae. Thus, the suborder Eimeriidea naturally breaks up into four families (not counting the questionable family Dobelliidae): Selenococcidiidae, Eimeriidae, Lankesterellidae, and Aggregatidae. The Eimeriidae divides into six subfamilies (Hoare, 1933) on the basis of the number of spores in the oocyst. The genera within each subfamily are determined by the number of sporozoites in the oocyst (or spore). Therefore, the principle of classification according to

the oocyst structure, which was introduced by Schneider, Minchin, Leger, and others, finds its application in the subfamilies and genera. Orlov's (1947) proposal to divide this family into two subfamilies - Asporocystinae and Sporocystinae - cannot be considered good because of the tremendous bulk and heterogeneity of the second subfamily.

It is possible to accept, with some alterations and additions, the system of Hoare (1933) for the family Eimeriidae (see table).

Classification of the Family Eimeriidae

No.	Subfamilies and genera	No. of Spores	No. of Sporozoites	
			in spores	in oocysts
I	Subfamily Cryptosporidiinae, Hoare	None		
	Genus Cryptosporidium			4
	Genus Pfeifferinella			8
	Genus Tyzzeria (?)			8
2	Subfamily Caryosporinae, Wenyon			
	Genus Mantonella	I	4	4
	Genus Caryospora		8	8
3	Subfamily Cyclosporinae, Wenyon			
	Genus Cyclospora	2	2	4
	Genus Isospora (=Diplospora)		4	8
	Genus Dorisiella		8	16
4	Subfamily Eimeriinae, Wenyon			
	Genus Eimeria (Globidium)*	4	2	8
	Genus Wenyonella		4	16
	Genus Angeiocystis (?)		many	many
5	Subfamily Yakimovellinae, Gouseff			
	Genus Yakimovella	8	many	many
6	Subfamily Barroussiinae, Wenyon			
	Genus Barroussia	many	I	many
	Genus Echinospora (?)		I	many
	Genus Pythonella		4	many
	Genus Caryotropha		12	many

* The genus Globidium is probably a synonym of the genus Eimeria (Doflein and Reichenow, 1953).

Our knowledge about the suborder Haemosporidia has increased considerably in recent years. There is new data about the exo-erythrocytic cycle of the genus Plasmodium and about the sexual process and sporogony of Leucocytozoon and others. In various species of Plasmodium, the exo-erythrocytic schizonts were found in the cells of the hemopoietic system, of the reticulo-endothelial system, and of the liver. To a considerable degree, this has drawn the Plasmodium together with the other genera of this suborder. The sexual process and sporogony were found to be

in the vector. The latter are the dipteran insects: <u>Anopheles</u> for <u>Plasmodium</u>, <u>Simulium</u> for <u>Leucocytozoon</u>, and the flies <u>Lynchia</u> and <u>Olfersia</u> for <u>Haemoproteus</u>.

In the family Haemoproteidae, schizogony occurs only exo-erythrocytically, and the gamonts are found in the peripheral blood cells. In the other family, Plasmodiidae, there are two stages of schizogony, exo-erythrocytic and erythrocytic, which differ in specific details in the various members of the genus <u>Plasmodium</u>. Schizonts and gamonts develop in the erythrocytes. The Haemoproteidae parasitize reptiles and birds, and the Plasmodiidae parasitize mammals. Probably several genera which parasitize mammals should be included with <u>Haemoproteus</u> and <u>Leucocytozoon</u> in the first family. These are <u>Hepatocystis</u> (parasites of monkeys and bats) and Nycteria and Polychromophilus (parasites of bats). In these, only the gamonts develop in the erythrocytes; in the first two genera, schizogony occurs in the liver cells, and in the last genus, in the cells of the reticulo-endothelial system of internal organs (Garnham, 1953). Further investigation is necessary to clarify the relationship of these genera with the other members of the suborder. A more detailed discussion of the systematics of the Haemosporidia will not be given here because it is a large and independent problem and should be worked out in a separate article.

On the basis of the reasons that I have stated above, it is possible to consider as correct the following taxonomic system of the Sporozoa[1].

<u>CLASS SPOROZOA LEUCKART</u>, 1879

Class Sporozoa (Poche, 1913; Hartmann, 1923; Wenyon, 1926; Yakimov, 1931; Epshtein, 1931).

Class Telosporidia (Hartmann, 1907; Calkins, 1926, 1933; Hall, 1953).

Subclass Cytosporidia (Labbé, 1897). Ectospora (Mesnil, 1899).

Subclass Telosporidia (Schaudinn, 1900; Doflein, 1901, 1902, 1909; Doflein and Reichenow, 1929, 1953; Kudo, 1931, 1946; Dogel', 1937, 1951; Hyman, 1940; Hoare, 1949; Boyd, 1949).

Subphylum Sporozoa (Grassé, 1953).

1. <u>Subclass Gregarinina Dufour, 1828</u>

Order Gregarinida (Doflein, 1901, 1902, 1909; Doflein and Reichenow, 1929, 1953; Calkins, 1912; Hartmann, 1923; Kudo, 1931, 1946; Dogel', 1937, 1951).

Subclass Gregarinida (Wenyon, 1926; Yakimov, 1931; Calkins, 1926, 1933; Hall, 1953).

Class Gregarinomorpha (Grassé, 1953).

1. <u>Order Eugregarinida Léger, 1900</u> (Doflein, 1901)

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[1]The names of the systematic groups and the authors who presented them are placed together in one of the groups of the given system on the basis of content. In the original article, Cheissin pointed out the fact that those names were in brevier type. In this translation, the taxa which Cheissin accepts are <u>double-underlined</u>, while their synonyms are not. V.I.]

Suborder Eugregarinaria (Doflein, 1901, 1909; Doflein and Reichenow, 1929, 1953; Dogel', 1937, 1951).

Suborder Gregarinea (Poche, 1913).

Order Eugregarina (Wenyon, 1926; Yakimov, 1931; Grasse, 1953; Hall, 1953).

2. Order Schizogregarinida Léger, 1910

Suborder Schizogregarinina (Minchin, 1903; Léger, 1900; Doflein and Reichenow, 1929, 1953; Dogel', 1937, 1951).

Suborder Amoebosporidia (Doflein, 1902).

Suborder Schizocystinea (Poche, 1913).

Order Schizogregarina (Wenyon, 1926; Hall, 1953); Archigregarina plus Neogregarina (Grassé, 1953).

II. Subclass Coccidiomorpha Doflein, 1901

Order Coccidiomorpha (Doflein, 1901, 1902, 1909, 1916).

Order Eimeriidea (Poche, 1913).

Order Cocciidia (Doflein and Reichenow, 1953).

Subclass Coccidiomorpha (Wenyon, 1926; Calkins, 1926; Yakimov, 1931).

Class Coccidiomorpha (Grassé, 1953).

Orders Coccidia plus Haemosporidia (Doflein and Reichenow, 1929; Hartmann, 1923; Kudo, 1931, 1946; Dogel', 1937, 1951; Bhatia, 1939; Hyman, 1940; Hoare, 1949; Boyd, 1949.

Subclasses: Prococcidia plus Eucoccidia (Grassé, 1953); Coccidia plus Haemosporidia (Hall, 1953).

1. Order Protococcidia new order

Eucoccidium dinophili (Grell, 1953)

2. Order Adeleida Léger, 1911

Tribe Adeleidae (order Eimeriidea) (Poche, 1931).

Suborder Adeleidea (order Coccidia) (Hartmann, 1923; Doflein and Reichenow, 1929, 1953; Dogel', 1937).

Order Adeleidea (Wenyon, 1926; Yakimov, 1931; Grassé, 1953; Hall, 1953).

Family Adeleidae Léger, 1911

Family Haemogregarinidae Wenyon, 1926

3. Order Coccidiida Labbé, 1899

Suborder Eimeriidea plus order Haemosporidia (Doflein and Reichenow, 1929).

Suborder Eimeriidea plus suborder Haemosporidia (Doflein and Reichenow, 1953).

Order Eimeriidea plus Prococcidium (Grassé, 1953).

Order Coccidiida (Wenyon, 1926) (without Piroplasmidea).

1. Suborder Eimeriidea Léger, 1911

Tribe Eimerioidae plus suborder Selenococcidia (Poche, 1913).

Suborder Eimeriidea (Doflein and Reichenow, 1929, 1953; Wenyon, 1926).

Suborder Coccidia (Doflein, 1909).

Suborder Holoeimeriidea plus Prococcidia (Grassé, 1953).

> **Family Eimeriidae Poche, 1913.**
>
> **Family Lankesterellidae Reichenow, 1921.**
>
> **Family Aggregatidae (Labbé) Reichenow, 1921.**
>
> **Family Selenococcidiidae Poche, 1913.**

2. Suborder Haemosporidiidea Danilevskij, 1885

Order Haemosporidia (Doflein and Reichenow, 1929; Dogel', 1937, 1951; Boyd, 1949; Hoare, 1949).

Suborder Haemosporidia (Doflein and Reichenow, 1953; Wenyon, 1926; Grassé, 1953).

Order Plasmodiidea (Hall, 1953).

> **Family Haemoproteidae Doflein, 1916.**
>
> **Family Plasmodiidae Mesnil, 1908.**

It should be mentioned that in the above classification of the Sporozoa, a large group of blood protozoa, Piroplasmidea, has been left out. The position of this group, which causes serious disease in domestic animals, is not clear because it has been inadequately studied; and the data regarding the life cycle of this group are extremely conflicting. For example, Dennis (1932) describes in detail the sexual process of Babesia bigemina, but Regendanz and Reichenow (1933) deny the presence of this process in B. canis. Different forms of the sexual process of Babesiella bovis and Piroplasma caballi are described by Petrov (1939) and Tsaprun (1953) [sic] , and by Sergent, Donatien, Parrot, and Lestoquard (1945) for Theileria.

The process of agamous multiplication is still uncertain. Some authors describe only binary fission. Others describe schizogony in the vertebrate host

(Jvanič, 1937, 1942; Kolabskiĭ, 1954), or in the carrier (Petrov, 1939; Abramov, 1955). There are several opinions regarding the morphology of the piroplasmids. Breinl and Hinkle (1908) detected flagella; others have not seen them, but a blepharoplast has been described (Dennis, 1932). Due to these discrepancies, the taxonomic system of the piroplasmids cannot be determined definitely. Hartmann and Jollos (1910), Léger and Duboscq (1910), Lühe (1913), and du Toit (1918) attached them to the flagellates, order Binucleata. Doflein (1909) and França (1909) put them in the class Sporozoa; and Poche (1913) and Calkins (1912) put them in the order Haemosporidia, suborder Acytosporea, together with Plasmodium and Haemoproteus. Dennis (1932) considers the piroplasmids intermediate forms between the haemoflagellates and the haemosporidia, and Regendanz and Reichenow (1933) believe they are closer to the Rhizopoda.

In their texts on Protozoology, Wenyon (1926), Yakimov (1931), and Brumpt (1936)consider the Piroplasmidea a suborder (equal with Haemosporidia) of the order Coccidia; Hall (1953) considers it an order of the subclass Haemosporidia, Curasson (1943) a suborder in the order Haemosporidia, and finally, Grassé as "sporozoa of an uncertain nature".

With the present knowledge of these protozoa, only an assumption, not a final decision, can be made regarding their systematic position. It seems to me that neither the Piroplasmidae nor the Theileriidae has the characteristics of the Sporozoa in the sexual process, even if the many contradictory investigations are taken into consideration. In any case, since the process of gametogenesis has not been observed, these two families do not belong with the gregarines or the coccidia; and since they do not have the typical characteristics, they should not be placed in the class Sporozoa. In order to determine the taxonomic position of the piroplasmids, the life cycle, especially the stages in the vector, must be studied further. These investigations must be carried out without bias and without the desire to make the life cycle fit at any price an existing one in the Sporozoa.

In conclusion, we will look briefly at possible phylogenetic relations within the class Sporozoa. The Sporozoa possess some structural characteristics which draw them together with the flagellates. For example, the merozoites resemble the leptomonads; the flagellated microgametes are similar to Bodo, and the sexual process is similar to that in the phytomonads. Meanwhile, transitional forms which would link the free-living flagellates and the sporozoa have not been found; therefore, opinions about the phylogeny of the Sporozoa are still in the realm of conjecture.

Probably some of the ancestors of the Sporozoa were obscure flagellates which possessed a more primitive life cycle similar to that observed in some of the contemporary phytomonads. These forms have an optional sexual cycle; the vegetative stages are constantly dividing, and the number of agamous generations is not fixed. The sexual process occurs in the external environment. The vegetative individuals, or else their direct unaltered generations, fulfill the role of the gametes by acquiring a sexual differentiation. The progamous period is absent. Isogamy occurs, since the male and female gametes differ only physiologically and not morphologically. The zygote encysts, and reduction division takes place during the metagamous period, which results in a few vegetative individuals. Such a general scheme of metagenetic development remains in the transition to parasitism; however, under various conditions of life, new traits emerge in different individuals.

First of all, the alternation of generations becomes stable due to the fact that the sexual process is now obligatory in the life cycle of the Sporozoa[2]. The metagamous stage of the cycle increases considerably in significance, assuming the task of separation from one host and infection of another. The development of the progamous period ensures maximum fertility. This is promoted by a considerable increase in the trophic function of the vegetative stages. In some cases, these stages accumulate large quantities of nutrients, increase greatly in size, and lose the ability to reproduce asexually. However, they acquire the means of forming a large number of gametes at the expense of the accumulated nutrients. In other cases, the vegetative stage utilizes the nutritive material for augmenting asexual reproduction (schizogony), and leads to the increase in fertility.

Probably the Sporozoa originally became adapted to parasitism in the intestine of aquatic invertebrates. The range of hosts widened with the inclusion of terrestrial invertebrates and vertebrates. The most primitive forms lived in the lumen of the intestine. As the Sporozoa evolved, their relationship with the host increased, and intracellular forms finally appeared. In the beginning, these forms constituted a small part of the life cycle and were transsitory, but later they made up a large part of the cycle and were permanently intracellular.

Most of the gregarines retained this most ancient characteristic of inhabiting the intestinal lumen. Only a small group of schizogregarines transferred partially to an intracellular location in various invertebrate hosts. At the same time, only a few of the most primitive coccidia retained extracellular parasitism, while the majority of the species transferred to a tissue mode of life, both in the invertebrate and vertebrate hosts.

The metagamous stage of the life cycle, which is in general similar in the gregarines and the coccidia was evidently determined first. This stage ensures the distribution of the parasite among the hosts and strengthens the parasitic mode of life. The development of maximum fertility is realized in different ways in the gregarines and the coccidia. In the gregarines a great number of gametes are formed at the expense of a large accumulation of nutrients in the vegetative stage (which has lost its ability to reproduce asexually). The gamonts of the sexes take up equal amounts of the nutrients, so that gametogenesis is similar in the male and the female, and the resulting gametes differ very little. The conditions for the formation of macrogametes and microgametes are not present. Since the gamonts are together under a common membrane, it is possible for the fertilization of iso- or anisogametes to take place, even though their motility is limited and numerical advantage on the part of the male is absent. Multiple division appears with the intracellular development of the vegetative stages of the schizogregarines (Selenidium and others). It is seen also in those schizogregarines which develop in the body cavity (Ophryocystis and others). It is possible that schizogony developed in this case because of the sparse production of each gamont (one, two, four, 16 gametes). Schizogony compensates for the small number of gametes produced by increasing the number of gamonts themselves. The gregarines, with such weak sexual reproduction, undoubtedly would not exist without schizogony.

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[2]The elimination of gamont formation (Huff and Bombell, 1934, and others), as in the Plasmodium life cycle, is encountered very rarely, and is the exception rather than the rule.

Increase in productivity is achieved differently in the Coccidiomorpha than in the gregarines. The most primitive forms of coccidia developed extracellularly. The coccidium, <u>Eucoccidium dinophili</u>, from the body cavity of Dinophilus, indicates this to some degree. Its life cycle partially reflects the evolution of the coccidia. The vegetative stages, the gamonts, do not unite in syzygy and somewhat determine the characteristics of the progamous period. The nutrients accumulate unequally in the gamonts of the two sexes. The macrogamont grows into a macrogamete, and the microgamont produces from four to 32 flagellated microgametes. Fertilization is ensured in the body cavity of the worm because of the large number of microgametes (compared with the macrogametes) and their considerable motility. The high productivity of the metagamous period compensates for the absence of schizogony. In the oocyst, up to 250 spores with six sporozoites in each are formed. Thus, if the worm ingested just one oocyst, nearly 1500 sporozoites would be liberated.
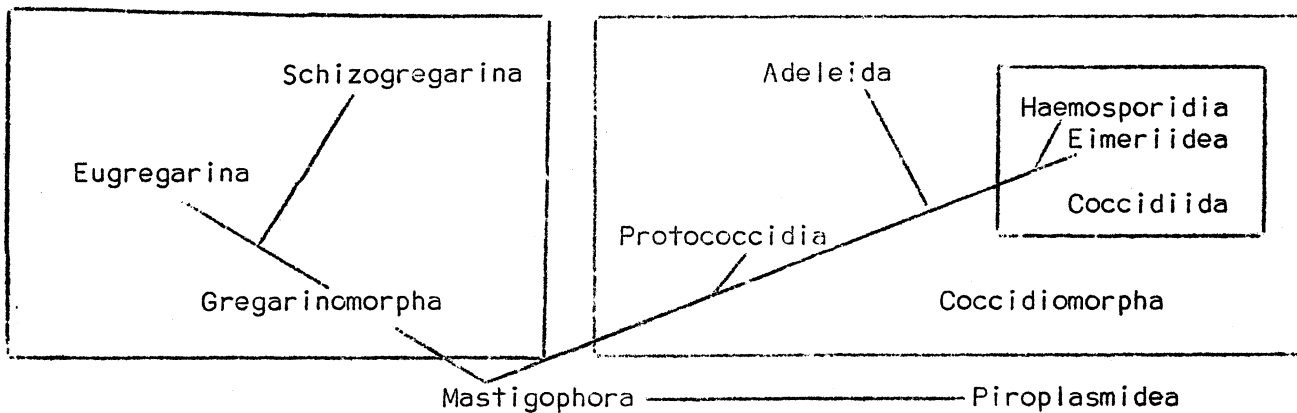
In all the other coccidia, the vegetative stages develop intracellularly by schizogony, which leads to autoinvasion of the host tissues. Considering the large number of merozoites in each agamous generation, we can imagine the importance of this process for augmenting the propagation of the parasite. For example, 800,000 oocysts are produced in a rabbit infected with one oocyst of <u>E</u>. <u>magna</u>, (Khe'isin, 1940, 1947). Therefore, in contradistinction to the gregarines, a large number of macrogametes is produced by formation of many macrogamonts from merozoites of one to several generations.

During the evolution of the coccidia, the microgametes increased in numbers and motility, ensuring fertilization of gametes dissociated in the host tissues. The gametes develop intracellularly in all the Coccidida except the Haemosporidia. In the latter, they form in the intestinal lumen of the insect. In contrast to the tissue coccidia, their microgametes are flagellum-shaped and few in number. Probably this second characteristic is due to the location of the gametes. Perhaps, since the gametes develop extracellularly, this should be considered a peculiar recapitulation in the life cycle of the blood sporozoa. If the Haemosporidia originated from the intestinal coccidia (Dogel', 1947, 1951), the above assumption concerning the decrease of microgametes in the Haemosporidia is quite possible.

The other line of development is observed in the Adeleida. Here the gamonts and gametes are intracellular, and only a small number of microgametes are produced. Fertilization is possible, since the macro- and microgamonts develop in close contact with one another. The sexual process in the order Coccidiida is probably more perfect than that in the Adeleida. The fact that there is a larger number of species in the Coccidiida than in the Adeleida significantly supports this.

Many authors have noted the resemblance of syzygy in the adeleids and the gregarines, but this similarity is purely superficial. In the adeleids, the union of the gamonts is oogamy and represents a secondary process which produces a small number of microgametes that develop intracellularly. In the gregarines, syzygy occurs as the primary process, establishing iso- or anisogamy which occurs extra-cellularly.

On the basis of the reasons stated above, a scheme of phylogenetic interrelations in the class Sporozoa is presented in the following Chart:

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                                                                    ┌─────────────────┐
  ┌────────────────────────────┐  ┌──────────────────────────────│ Haemosporidia   │──┐
  │                            │  │  Adeleida                     │  / Eimeriidea   │  │
  │   Schizogregarina          │  │                               │ /               │  │
  │         /                  │  │                               │/  Coccidiida    │  │
  │        /                   │  │                               └─────────────────┘  │
  │   Eugregarina              │  │                                                     │
  │                            │  │      Protococcidia                                  │
  │   Gregarinomorpha          │  │                              Coccidiomorpha        │
  └────────────────────────────┘  └─────────────────────────────────────────────────┘
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Mastigophora ———————————————— Piroplasmidea

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