COCCIDIA, an important order of Sporozoa Ectospora, parasites possessing certain very distinctive characters. With one or two possible exceptions, they are invariably intracellular during the entire trophic life of the individual. They always attack tissue-cells, usually of an epithelium, and never blood-corpuscles. Correlated with the advanced degree of parasitism, there is a complete absence of specialization or differentiation of the cell-body, and the trophozoite is quite incapable of any kind of movement. In all cases, so far as known, the life-cycle is digenetic, an asexual generation (produced by schizogony) alternating with a sexual one (gametogony). After conjugation of two highly-differentiated gametes has taken place, a resistant oocyst is formed, which provides for the dispersal of the species: inside this sporogony (spore- and sporozoite-formation) goes on.

Hake (1839) was, perhaps, the first to describe a Coccidian, but he regarded the parasites as pathological cell-products. In 1845 N. Lieberkühn pointed out the resemblances *History.* to Gregarines, with which organisms he considered Coccidia to be allied. A year later, H. Kloss proved the existence of similar parasites in the snail, and attempted to construct their life-history; this form was subsequently named *Klossia helicina* by A. Schneider. The asexual part of the life-cycle was first described by Th. Eimer in 1870, for a Coccidian infesting the mouse, which was afterwards elevated by Schneider into a distinct genus *Eimeria*. The generic name *Coccidium* was introduced by R. Leuckart in 1879, for the parasite of the rabbit. It was many years, however, before the double character of the life-cycle was realized, and the ideas of L. and R. Pfeiffer, who first suggested the possibility of an alternation of generations, for a long time found no favour. In the first decade of the 20th century great progress was accomplished, thanks largely to the researches of F. Schaudinn and M. Siedlecki, who first demonstrated the occurrence of sexual conjugation in the group; and the Coccidian life-history is now one of the best known among Sporozoa.

Coccidia appear to be confined[1] to four great phyla, Vertebrates,

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[1] A curious organism, parasitic in a gregarine, has lately been described by Dogiel as a coccidian, and termed *Hyalosphaera*.

Molluscs, Arthropods and Annelids; the first named group furnishes by far the most hosts, the parasites being frequently met with in domestic animals, both birds and mammals. Following *Habitat: effects on host.* from the casual method of infection, the epithelium of the gut or of its appendages (*e.g.* the liver [Plate I., fig. 1]) is a very common seat of the parasitic invasion. But in many cases Coccidia are found in other organs, to which they are doubtless carried by lymphatic or circulatory channels. In Molluscs, they often occur in the kidneys (fig. 2); in Insects, they are met with as " coelomic " parasites, the fat-bodies, pericardial cells, &c., being a favourite habitat; even the testis is not free from their attentions in one or two instances, though the ovary appears always immune.

The parasite invariably destroys its host-cell completely. The latter is at first stimulated to abnormal growth and activity and becomes greatly hypertrophied, the nucleus also undergoing karyolytic changes (fig. 4). The fatty materials elaborated by the host-cell are rapidly used up by the Coccidian, as nourishment; and at length the weakened and disorganized cell is no longer able to assimilate but dies and is gradually absorbed by the parasite, becoming reduced to a mere enclosing skin or envelope. In some cases (ex. *Cyclospora caryolytica* of the mole) the parasite is actually intranuclear, the nucleus becoming greatly swollen and transformed into a huge vacuole containing it.

The effects of a Coccidian infection upon the host as a whole depend largely upon the extent to which endogenous multiplication of the parasites takes place. On the one hand, schizogony may be so limited in extent as not to cause appreciable injury to the host. This seems to be often the case in forms infecting Molluscs and Arthropods. On the other hand, where schizogony is rapid and prolonged, the results are often serious. For, although any one individual only causes the death of a single host-cell, yet the number of the parasites may be so enormously increased by this means, that the entire affected epithelium may be overrun and destroyed. Thus are occasioned grave attacks of coccidiosis, characterized by severe enteritis and diarrhoea, which may end fatally. In the case of the Vertebrates, secondary causes, resulting from the stoppage of the bile ducts, also help to produce death. There is, however, one factor in the endangered animal's favour. Schizogony cannot go on indefinitely; it has a limit, dependent upon the supply of host-cells, and consequently of nutriment, available. As this shows signs of becoming exhausted, by the rapid multiplication of the parasites, the latter begin to make preparations for the exogenous cycle, inaugurated by gametogony. When conjugation has taken place and sporogony is begun, the danger to the host is at an end. So that, if the acute stage of the disease is once successfully passed, the regenerative capacity of the epithelium may be able to restore something like equilibrium to the deranged metabolism in time to prevent collapse.

Coccidium schubergi, parasitic in the intestine of a centipede (*Lithobius forficatus*), may be taken as an example of a Coccidian *Morphology and life-history.* life-history (see Schaudinn, 1900): some of the more important variations exhibited by other forms will be noted afterwards. The trophozoite, or actively-growing parasite, is an oval or rounded body (fig. 3, I.). The general cytoplasm shows no differentiation into ectoplasm and endoplasm; it is uniformly alveolar in character. The nucleus is relatively large, and possesses a distinct membrane and a well-marked reticulum in which are embedded grains of chromatin. Its most conspicuous feature is the large deeply-staining karyosome, which consists of the greater part of the chromatin of the nucleus intimately bound up with a plastinoid basis. When fully grown, the trophozoite (now a schizont) undergoes schizogony. Its nucleus divides successively to form a number of nuclei, which travel to the periphery, and there become more or less regularly disposed (fig. 3, II. and III.). The protoplasm in the neighbourhood of each next grows out, as a projecting bud, carrying the nucleus with it. In this manner are formed a number of club-shaped bodies, the merozoites, which are at length set free from the parent-body (IV.), leaving a certain amount of residual cytoplasm behind. By the rupture of the disorganized host-

cell,[1] the fully-formed merozoites are liberated into the intestinal lumen, and seek out fresh epithelial cells. Each is more or less sickle-shaped, and capable of active movements. Once inside a new host-cell, the merozoite grows to a schizont again.

After this course has been repeated several times, gametogony sets in, the trophozoites growing more slowly and becoming the parent-cells of the sexual elements (gametocytes), either male individuals (microgametocytes) or female ones (megagametocytes). A microgametocyte (fig. 3, VI. ♂) is characterized by its dense but finely reticular or alveolar cytoplasm, very different from the loose structure of that of a schizont. The male elements (microgametes) are formed in a manner essentially comparable to that in which the formation of merozoites takes place. Although the details of the nuclear changes and divisions vary somewhat, the end-result is similar, a number of little nuclear agglomerations being evenly distributed at the surface (VII. ♂). Each of these elongates considerably, becoming comma-shaped and projecting from the gametocyte. Nearly all the body of the male gamete (VIII. ♂) consists of chromatin, the cytoplasm only forming a very delicate zone or envelope around the nucleus. From the cytoplasm two long fine flagella grow out, one of which originates at the anterior end, the other, apparently, at the hinder end, acting as a rudder; but it is probable that this also is developed at the anterior end and attached to the side of the body. By means of their flagella the numerous microgametes break loose from the body of the microgametocyte and swim away in search of a female element.

A megagametocyte (VI. ♀) is distinguished by its rather different shape, being more like a bean than a sphere until ripe for maturation, and by the fact that it stores up in its cytoplasm quantities of reserve nutriment in the form of rounded refringent plastinoid grains. Each female gametocyte gives rise to only a single female element (megagamete), after a process of nuclear purification. The karyosome is expelled from the nucleus into the cytoplasm, where it breaks up at once into fragments (VII. ♀). Meanwhile the gametocyte is becoming spherical, and its changes in shape aid in setting it free from the shrivelled host-cell. The fragments of the karyosome, which are, as it were, squeezed out to the exterior, exert a powerful attraction upon the microgametes, many of which swarm round the now mature megagamete. The female nucleus (pronucleus) approaches the surface of the cell (VIII. ♀), and at this spot a little clear cytoplasmic prominence arises (cone of reception). On coming into contact with this protuberance (probably attracted to it by the female pronucleus), a microgamete adheres. Partly by its own movements and partly by the withdrawal of the cone of attraction, the male penetrates into the female element and fertilization is accomplished. Only one microgamete can thus pass into the megagamete, for immediately its entry is effected a delicate membrane is secreted around the copula (zygote), which effectually excludes other less fortunate ones. This membrane rapidly increases in thickness and becomes the oocyst (IX.), and the copula is now ready to begin sporogony.

Sporogony goes on indifferently either inside the host or after the cyst has been passed out with the faeces to the exterior. The definitive nucleus of the zygote (resulting from the intimate fusion of the male and female pronuclei, by means of a somewhat elaborate " fertilization-spindle " [X.]) gives rise by successive direct divisions to four nuclei (XII.), around which the protoplasm becomes segregated; these segments form the four sporoblasts. Around each sporoblast two membranes are successively secreted (exospore and endospore), which constitute the sporocyst (XIII.); the sporocyst and its contents forming the spore. The nucleus of each spore next divides, again directly, and this is followed by the division of the cytoplasm. As a final result, each of the four spores contains two germs (sporozoites), and a certain amount of residual protoplasm (fig. 3, XIV.); this latter encloses a viscid, vacuole-like body, which aids in the subsequent dehiscence of the sporocyst. On being eaten by a fresh host, the wall of the oocyst is dissolved at a particular region by the

[1] It is important to note that in schizogony there is never any cyst or cyst-membrane formed around the parasite.
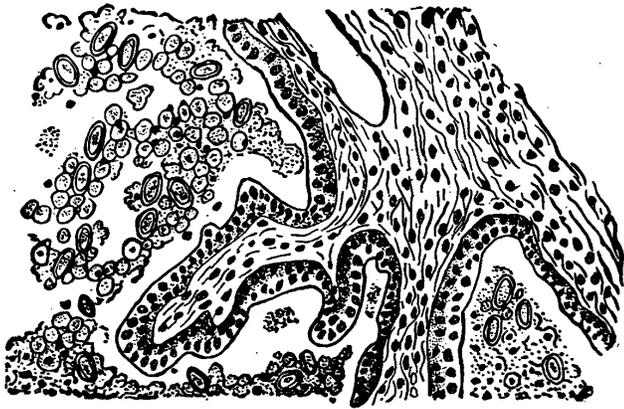
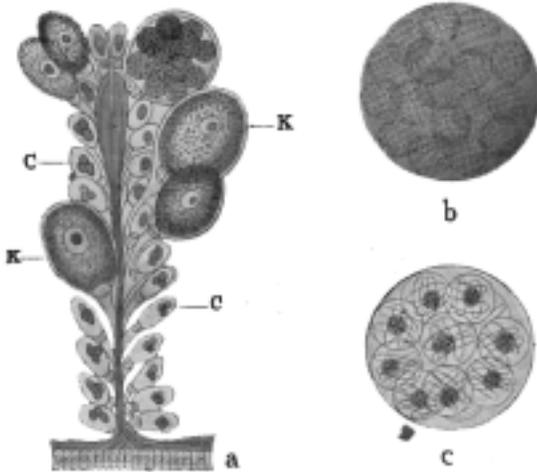FIG. 1.—SECTION THROUGH RABBIT'S LIVER, INFECTED WITH *COCCIDIUM CUNICULI.* (AFTER THOMA.)

FIG. 2.—*KLOSSIA HELICINA,* FROM KIDNEY OF *HELIX HORTENSIS.*

a, Portion of a section of the kidney showing normal epithelial cells containing concretions (*c*), and enlarged epithelial cells containing the parasite (*k*) in various stages; *b,* cyst of the *Klossia* containing sporoblasts; *c,* cyst with ripe spores, each enclosing four sporozoites and a patch of residual protoplasm. (From Wasielewski, after Balbiani.)
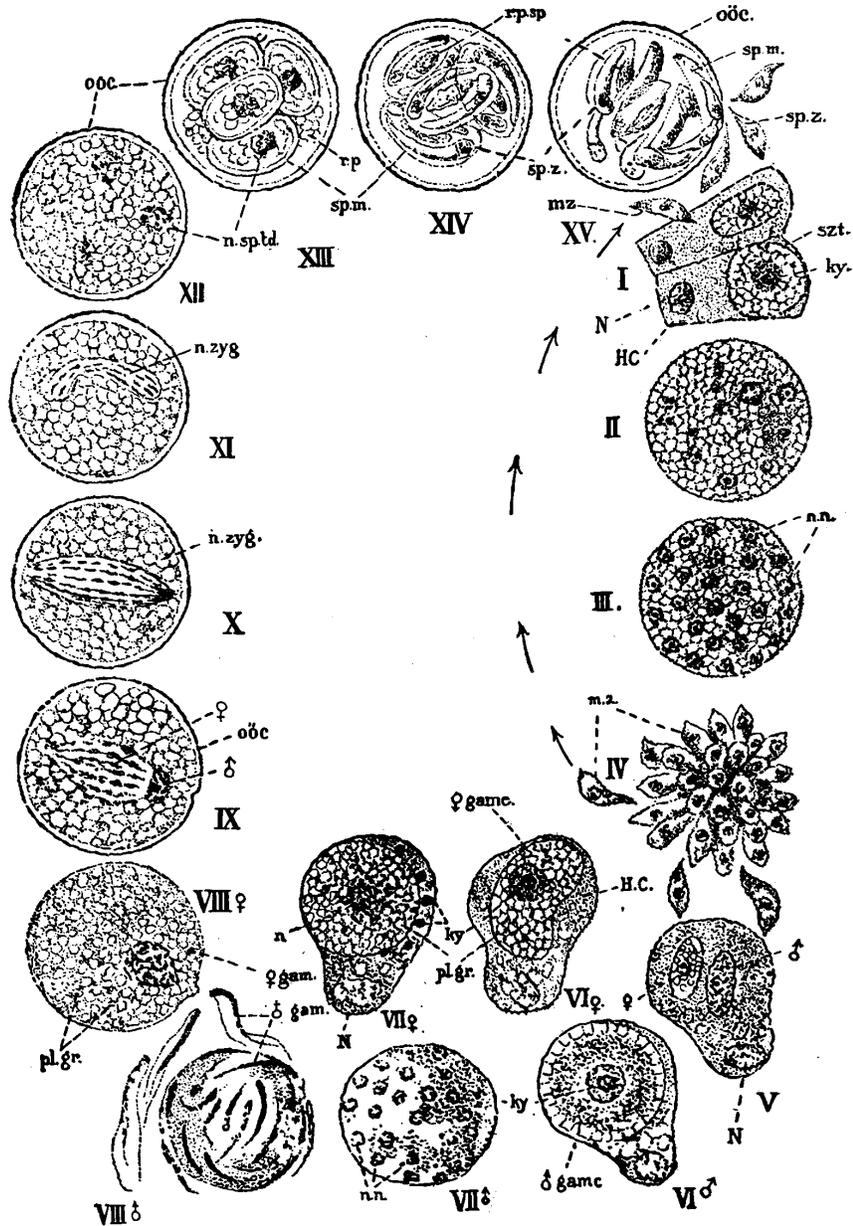

FIG. 4.—PHASES OF *CARYOTROPHA MESNILII,* SIEDL. (PAR. *POLYMNIA NEBULOSA*).

FIG. 3.—THE LIFE-CYCLE OF *COCCIDIUM SCHUBERGI,* SCHAUD. (PAR. *LITHOBIUS FORFICATUS*). (FROM MIN-CHIN, AFTER SCHAUDINN.)

I.-IV represents the schizogony, commencing with infection of an epithelial cell by a sporozoite or merozoite. After stage IV the development may start again at stage I, as indicated by the arrows; or it may go on to the formation of gametocytes (V). V-VIII represents the sexual generation. The line of development, hitherto single (I-IV) becomes split into two lines—male (VI ♂, VII ♂, VIII ♂), and female (VI ♀, VII ♀, VIII ♀), culminating in the highly differentiated micro- and mega-gametes. By conjugation these two lines are again united. IX, X, show the formation of the zygote by fusion of the nuclei of the gametes. XI-XV, sporogony. *H.C,* host-cell; *N,* its nucleus; *mz,* merozoite; *szt,* schizont; *ky,* karyosome (or fragments of same); *n.n,* daughter-nuclei of schizont; *pl.gr,* plastinoid grains; *ooc,* oocyst; *n.zyg,* zygote-nucleus (segmentation-nucleus); *sp.m,* spore-membrane (sporocyst); *rp,* residual protoplasm of oocyst ("reliquat kystal"); *rp.sp,* residual protoplasm of spore ("reliquat sporal"); *sp.z,* sporozoite.
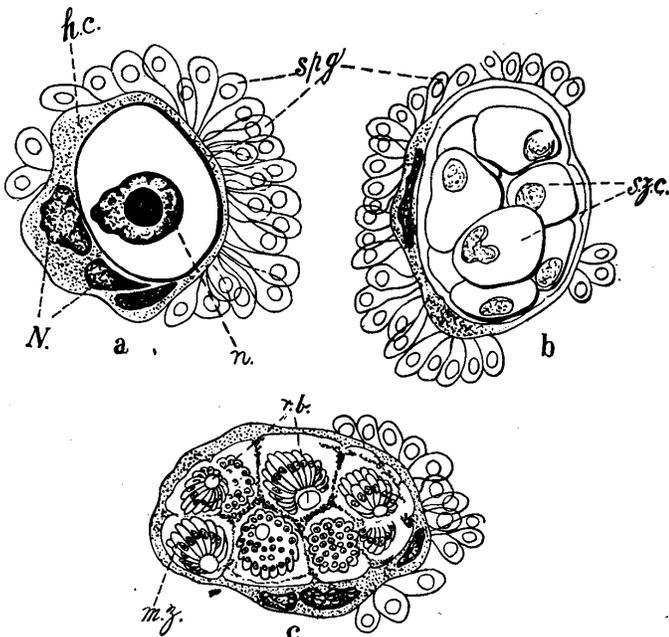
a, Young schizont in a cluster of spermatogonia; the host-cell (represented granulated) and two of its neighbours are greatly hypertrophied, with very large nuclei, and have fused into a single mass containing the parasite (represented clear, with a thick outline). The other spermatogonia are normal. *b,* Intracellular schizont divided up into schizontocytes (*c*), each schizontocyte giving rise to a cluster of merozoites arranged as a "corps en barillet"; *spg,* spermatogonia; *h.c,* host-cell; *N,* nucleus of host-cell or cells; *n,* nucleus of parasite; *szc,* schizontocyte; *mz,* merozoites; *r.b,* residual bodies of the schizontocytes. (From Minchin, after Siedlecki.)
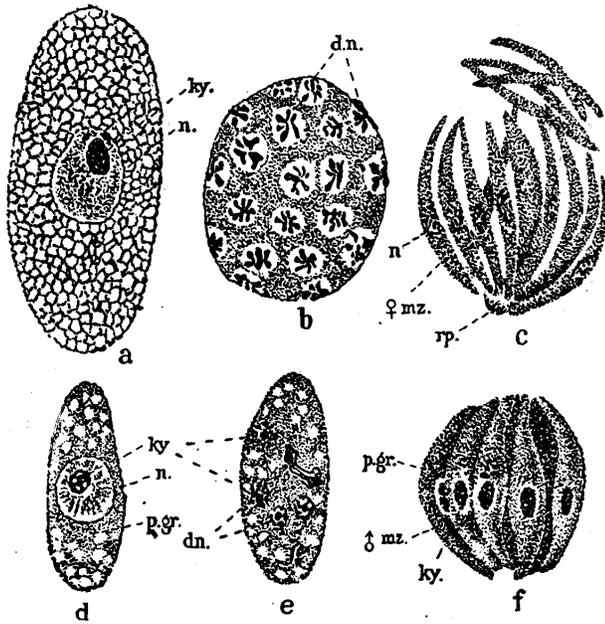
PLATE II.   COCCIDIA

FIG. 5.—SCHIZOGONY OF *ADELEA OVATA*, A. SCHN.
(PAR. *LITHOBIUS FORFICATUS*).

a-c, ♀ generation; *d-f*, ♂ generation. *a*, Full-grown ♀ schizont (*megaschizont*), with a large nucleus (*n*) containing a conspicuous karyosome (*ky*). *b*, Commencement of schizogony; the nucleus has divided up to form a number of daughter-nuclei (*d.n*). The karyosome of stage *a* has broken up into a great number of daughter-karyosomes, each of which forms at first the centre of one of the star-shaped daughter-nuclei; but in a short time the daughter-karyosomes become inconspicuous. *c*, Completion of schizogony; the ♀ schizont has broken up into a number of *megamerozoites* (♀ *mz*) implanted on a small quantity of residual protoplasm (*r.p.*). Each ♀ merozoite has a chromatic nucleus (*n*) without a karyosome. *d*, Full-grown ♂ schizont (*microschizont*), with nucleus (*n*), karyosome (*ky*), and a number of characteristic pigment-granules (*p.gr*). *e*, Commencement of schizogony. The nucleus is dividing up into a number of daughter-nuclei (*d.n*), each with a conspicuous karyosome (*ky*). *f*, Completion of schizogony. The numerous micro-merozoites (♂ *mz*) have each a nucleus with a conspicuous karyosome (*ky*) at one pole, and the protoplasm contains pigment-granules (*p.gr*) near the nucleus, on the side farthest from the karyosome. (From Minchin, after Siedlecki.)
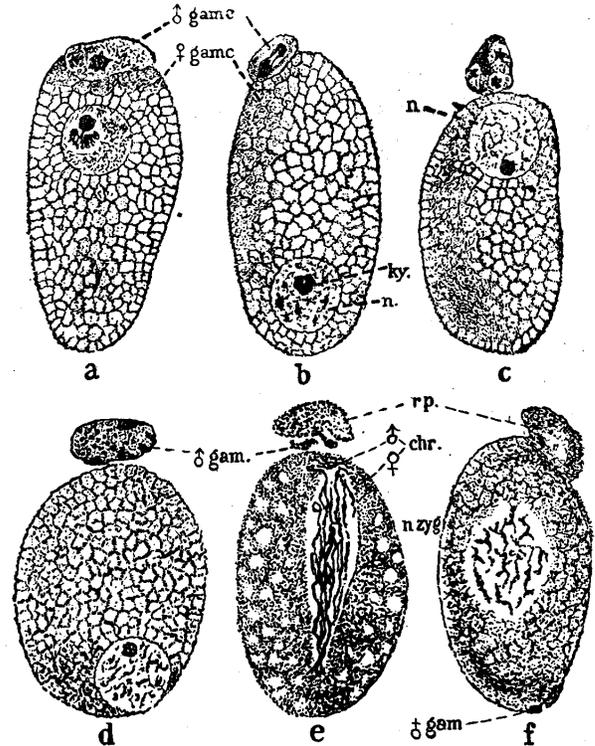

FIG. 6.—ASSOCIATION AND CONJUGATION IN *ADELEA OVATA*.

a, Young microgametocyte (♂ *gamc.*) attached to a megagametocyte (♀ *gamc.*). The nucleus of the microgametocyte gives rise to 4 daughter-nuclei (*c*) which become (*d*) 4 microgametes (♂ *gam.*). *e*, One of the microgametes penetrates the megagamete, which forms a fertilization-spindle composed of male and female chromatin (♂ and ♀ *chr.*). The other 3 microgametes and the residual protoplasm of the microgametocyte (*r.p.*) perish. The karyosome of the megagamete has disappeared, as such. *f*, Union of the chromatin of both elements, to produce the zygote-nucleus (*n.zyg.*). (From Minchin, after Siedlecki.)
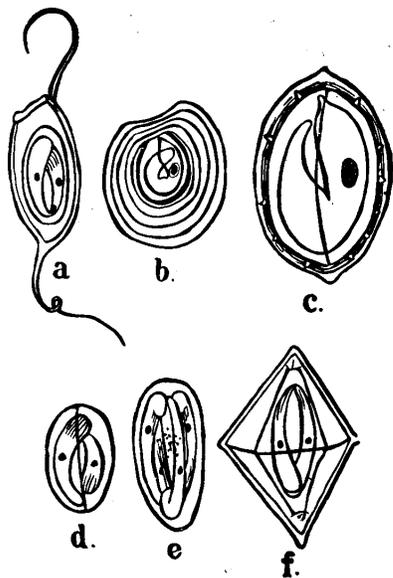

FIG. 7.—SPORES OF VARIOUS COCCIDIAN GENERA.

a, *Minchinia chitonis* (E.R.L.), (par. *Chiton*); *b*, *Diaspora hydatidea*, Léger (par. *Polydesmus*); *c*, *Echinospora labbei*, Léger (par. *Lithobius mutabilis*); *d*, *Goussia motellae*, Labbé; *e*, *Diplospora* (*Hyaloklossia*), *lieberkuhni* (Labbé), (par. *Rana esculenta*); *f*, *Crystallospora crystalloides* (Thél.), (par. *Motella tricirrata*). (From Minchin; *b* and *c* after Léger, the others after Labbé.)
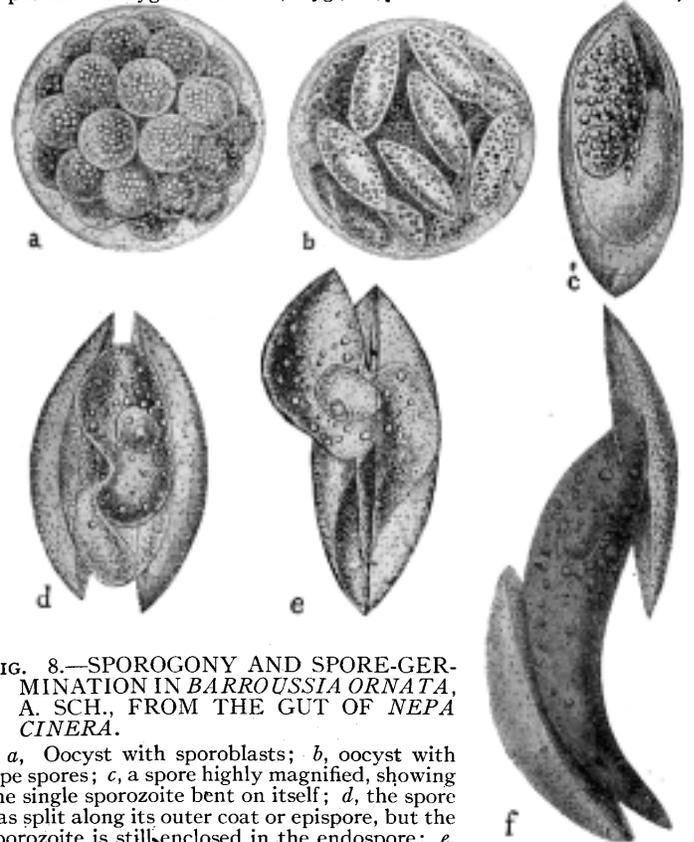

FIG. 8.—SPOROGONY AND SPORE-GERMINATION IN *BARROUSSIA ORNATA*, A. SCH., FROM THE GUT OF *NEPA CINERA*.

a, Oocyst with sporoblasts; *b*, oocyst with ripe spores; *c*, a spore highly magnified, showing the single sporozoite bent on itself; *d*, the spore has split along its outer coat or epispore, but the sporozoite is still enclosed in the endospore; *e*, the sporozoite, freed from the endospore, is emerging; *f*, the sporozoite has straightened itself out and is freed from its envelopes. (From Wasielewski, after A. Schneider.)

digestive juices, which are thus enabled to reach the spores and cause the rupture of the sporocysts. As the result of instructive experiments, Metzner has shown that it is the pancreatic and not the gastric juice by which this liberation of the germs is effected. The liberated sporozoites creep out and proceed to infect the epithelial cells. The sporozoites (XV.) are from $15-20 \mu$ long by $4-6 \mu$ wide; they are fairly similar to merozoites in form, structure and behaviour, the chief point of distinction being that they have no karyosome in the nucleus (cf. above).

Comparing the life-cycle of other Coccidia with that just described, a greater or less degree of modification is frequently met with. In the process of schizogony two orders of division sometimes occur; the parent-schizont first divides up into a varying number of rounded daughter-schizonts (schizontocytes), each of which gives rise, in the usual manner, to a cluster of merozoites,[1] which thus constitute a second order of cells. Siedlecki (1902) has found this to be the case in *Caryotropha mesnilii* (fig. 4), and Woodcock (1904) has shown that it is most probably really the same process which Smith and Johnson (1902) mistook for sporogony when originally describing their Coccidian of the mouse, *Klossiella*. In *Caryotropha*, a perfectly similar state of affairs is seen in the formation of microgametes from the microgametocyte; this is additionally interesting as showing that this process is neither more nor less than male schizogony.

Coming to the sexual generation, considerable variation is met with as regards the period in the life-history when sexual differentiation first makes its appearance. Sexuality may become evident at the very beginning of schizogony, as, *e.g.* in *Adelea ovata* (Siedlecki, 1899), where the first-formed schizonts (those developed from the sporozoites) are differentiated into male and female (micro- and mega-schizonts) (see Plate II., fig. 5). Correspondingly, the merozoites, to which they give rise, are also different (micro- and mega-merozoites). In one or two cases sexuality appears even earlier in the cycle, and has thus been carried still farther back.

The Coccidia, as a whole, have not developed the phenomenon of association of the sexual individuals prior to gamete-formation which is so characteristic of Gregarines. Their method of endeavouring to secure successful sporulation, and thus the survival of the species, has been rather by the extreme specialization of the sexual process. In place of many female elements, which the primitive or ancestral forms may be assumed to have had,[2] there is always, save possibly for one exception,[3] only a single relatively huge megagamete formed, which offers a comparatively easy goal for one of the many microgametes. Nevertheless in the effort to render fertilization absolutely certain, a few Coccidia have acquired (secondarily) the power of associating; a state of things which enables those forms, moreover, to effect an economy in the number of male gametes, only three or four being developed. Instances are seen in *Adelea mesnili* (Perez, 1903), *A. ovata* (fig. 6), and *Klossia helicina* (Siedlecki, 1899). It is very interesting to note that, in the two last cases, unless this association of the microgametocyte with the megagametocyte occurs, neither can the former produce male elements (microgametes) nor can the female individual maturate and become ready for fertilization. (Concerning this question of association see also GREGARINES.)

In sporogony, great variation is seen with respect to the number of spores and sporozoites formed; and, as in Gregarines, these characters are largely used for purposes of classification, under which heading they are better considered. Usually, the spores (fig. 7) are quite simple in outline, and not produced into

[1] The merozoites are frequently arranged like the staves of a barrel—whence the term *barillet*, which is frequently used.

[2] In *Cyclospora*, Schaudinn (1902) has noted certain abnormal cases of the persistence and further multiplication of the "reduction-nuclei" of the female element (*i.e.* the nuclear portions given off during maturation), followed by multiple fertilization. This occurrence points strongly to the conclusion that there were originally many female gametes (cf. also the sporoblasts of Gregarines).

[3] The remarkable forms parasitic in Cephalopods (of late known as *Eucoccidium*), if still ranked with the Coccidia, furnish an exception (see below).

spines or processes; exceptions are found, however, in a few instances (*e.g. Minchinia chitonis*). In one case (*Coccidium mitrarium*), the oocyst itself, instead of being spherical, is curiously shaped like a mitre.

The life-history as a whole is invariably undergone in a single host, *i.e.* there is no alternation of true hosts.[4] Schaudinn, in his work on the *Coccidia* of *Lithobius* (1900), showed that the oocysts expelled with the faeces may be eaten by wood-lice (*Oniscus*), but when this happens they pass through the intestine of the wood-louse unaltered, the latter not being an intermediate host but merely a carrier.

The order Coccidiidea is divided into four families, characterized by the number of sporocysts (if any) found in the oocyst.

Fam. ASPOROCYSTIDAE, Léger. No sporozoites are formed in the oocyst, the sporozoites being unenclosed (gymnospores). *Classification.*

Genus, *Légerella*, Mesnil. This genus actually conforms to Aimé Schneider's original definition of *Eimeria*, which was founded on what were really the schizogonous generations of other forms, then thought to be distinct. In view of the great confusion attending the use of this name, however, Mesnil (1900) has suggested the new one here adopted. Two species known, *L. nova* and *L. testiculi*, both from different species of *Glomeris*, a Myriapod; the former inhabits the Malpighian tubules, the latter the testis.

Fam. DISPOROCYSTIDAE, Léger. The oocyst contains 2 spores.

Genus 1. *Cyclospora*, A. Schneider. Spores dizoic, *i.e.* with two sporozoites. *C. glomericola*, from the intestinal epithelium of *Glomeris*, and *C. caryolytica*, from the intestinal epithelium of the mole, intranuclear.

Genus 2. *Diplospora*, Labbé. Spores tetrazoic. *D. lacazei*, from many birds, is the best-known species; and others have been described from different Sauropsida. *D. lieberkühni* is an interesting form occurring in the kidneys of the frog, which it reaches by way of the circulation.

Genus 3. *Isospora*, Schn. Spores polyzoic. Founded for *I. rara*, parasitic in the black slug (*Limax cinereo-niger*). Many authors consider that Schneider was mistaken in attributing many sporozoites to this form, and would unite with it the genus *Diplospora*.

Fam. TETRASPOROCYSTIDAE, Léger. The oocyst contains 4 spores.

Genus 1. *Coccidium*,[5] Leuckart. The spores are dizoic and the sporocysts rounded or oval. A very large number of species are known, mostly from Vertebrate hosts. *C. cuniculi* (= *C. oviforme*) from the rabbit (intestine and diverticula), but also occurring sometimes in other domestic animals; *C. falciformis*, from the mouse; *C. faurei* from sheep; and *C. schubergi*, from *Lithobius* (a centipede), are among the best-known forms. All of them may cause disastrous epidemics of coccidiosis.

Genus 2. *Paracoccidium*, Laveran and Mesnil. This genus is distinguished from *Coccidium* by the fact that the sporocysts become dissolved up in the oocyst, thus leaving the 8 sporozoites unenclosed, recalling the condition in *Légerella*. *P. prevoti*, unique species, from the frog's intestine.

Genus 3. *Crystallospora*, Labbé. Spores also dizoic, but having the form of a double pyramid. *C. crystalloides* from a fish, *Motella tricirrata*.

Genus 4. *Angeiocystis*, Brasil. Apparently 6 sporozoites, but the only species, *A. audouiniae*, has only been briefly described; from a Polychaete (*Audouinia*).

Fam. POLYSPOROCYSTIDAE, Léger. The oocyst contains numerous spores.

There are several genera with monozoic spores, characterized by variations in the form and structure of the sporocysts, *e.g. Barroussia*, Schn. (fig. 8), *Echinospora*, Léger, and *Diaspora*, Léger; most of these forms are from Myriapods.

Genus *Adelea*, Schn. Dizoic spores; sporocysts round or oval, plain. Several species are included in this well-known genus, among them being *A. ovata*, *A. mesnili*, *A. dimidiata*; most of them are parasitic in Insects or Myriapods.

Genus *Minchinia*, Labbé. Dizoic spores; the sporocysts are produced at each pole into a long filament. *M. chitonis*, from the liver of *Chiton* (Mollusca).

Genus *Klossia*, Schn. The spores are tetrazoic (or perhaps polyzoic). *K. helicina* from the kidney of various land-snails is the best-known form. Usually said to have 5 to 6 spores, but Mesnil considers that the normal number is 4, as is the case in another species, *K. soror.*

Genus *Caryotropha*, Siedlecki. Many spherical spores (about 20)

[4] Again with the exception of *Eucoccidium*.

[5] Purists in systematic nomenclature maintain that this name should be relinquished in favour of *Eimeria*, since the latter was the first legitimate generic name given to a Coccidian. But one reason against the use of *Eimeria* has been stated already (it should be used for *E. (Légerella) nova*, if anywhere); and in addition, the word *Coccidium* and its important derivatives are now so universally established that it would be little short of ridiculous to displace them.

each with 12 sporozoites. *C. mesnilii*, unique species, from the spermatogonial (testis) cells of *Polymnia* (a Polychaete). An interesting point in the schizogony is the formation of schizontocytes (see above).

A Coccidian parasitic in the kidneys of the mouse has been described by Smith and Johnson (1902) and named by them *Klossiella*, on the ground that it possessed many spores, each with about 20 sporozoites. Woodcock has shown, however, that the authors were in all probability dealing with a similar modification of schizogony to that which obtains in *Caryotropha*. The sporogony of this form (and hence its systematic position) remains at present, therefore, quite unknown.

There are several doubtful or insufficiently known genera, *e.g. Bananella, Goussia, Hyaloklossia, Gonobia, Pfeifferella* and *Rhabdospora*, many of which probably represent only schizogonous generations of other forms. (For information concerning these see Labbé, 1897.)

Lastly it remains to mention the extremely interesting forms parasitic in Cephalopods. For some years these have provided a fruitful source of discussion to systematists. Here it may be stated simply that their systematic position and nomenclature were thought to have been finally settled by the researches of Jacquemet (1903) and Lühe (1902) in the following terms:—

Genus *Eucoccidium*. Lühe (syn. *Légerina* Jacq.), Coccidia possessing polysporous oocysts and lacking schizogony, parasitic in Cephalopods. Two well-known species: *E. eberthi* (Labbé), (= *Benedenia* seu *Klossia e.* seu *octopiana*), parasitic in *Sepia*, which is tri- or tetra-zoic; and *E. octopianum* (Schn.), (syn. *Benedenia* seu *Klossia o.*) from *Octopus*, which is polyzoic, having 10 to 12 sporozoites. In both forms cysts containing megaspores and megasporozoites, and others containing microspores and microsporozoites are found, considered as representing sexual differentiation thrown back to the very earliest stages of the life-cycle.

Quite recently much additional light has been thrown upon our knowledge of these parasites, including a new one, *E. jacquemeti*. Moroff (1906) has shown that not one but many megagametes are formed, and fertilized by the microgametes. For this reason he regards them as Gregarines rather than Coccidia. Further, Léger and Duboscq (1906) have found that the characteristic coelomic parasites (*Aggregata*) of Crustacea, generally regarded as gymnosporous Gregarines (*i.e.* Gregarines in which the sporozoites are naked) constitute in reality nothing more or less than a schizogonous generation of these Cephalopodan parasites, which have thus an alternation of true hosts. The ripe sporocysts from the Cephalopod are eaten by a particular crab (*e.g. Portunus* or *Inachus*, according to the parasite), the sporozoites are liberated and traverse the mucous membrane of the intestine, coming to rest in the surrounding lymphatic layer. Here a large " cyst " is formed, projecting into the body-cavity, the contents of which give rise to a great number of merozoites. On the crab being devoured by the right species of Cephalopod, the merozoites doubtless give rise to the sexual generation again.

As the name *Aggregata* is much the older, and as, moreover, there is no longer any reason to retain that of *Eucoccidium*, these parasites must in future receive the former generic appellation. With regard to the various specific names, however, they remain quite unsettled until the life-history is properly worked out in different cases (see also GREGARINES).

It seems to the writer a much more open question than Moroff and Léger and Duboscq apparently suppose, whether these parasites are to be relegated to the Gregarines. For undoubtedly they have many Coccidian features, and on the other hand they differ in many ways from Gregarines. The chief feature of agreement with the latter order is the possession of many female gametes. As already said, there can be little doubt that this was the condition in the Coccidian ancestor, and it is by no means impossible that one or two forms existing at the present day remain primitive in that respect. On the other hand, the advanced character of the parasitism (the parasites remaining intracellular up to and including gamete-formation); the entire lack of the characteristic feature of association; the schizogony, which is only a very rare occurrence in Gregarines, and which, in the present case, strongly suggests the process in *Caryotropha* and *Klossiella*; and, last but not least, the varying number of the sporozoites (3 in one form, 10–15 in others), which is very different from the almost constant number (8) in Gregarines, are all characters in which these forms agree with Coccidia and not with Gregarines. Having regard to these points, the writer is inclined, for the present, to consider *Aggregata* as an offshoot rather from the Coccidian than from the Gregarine branch of the Ectosporan tree.

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