CONTRIBUTIONS

TO THE

DEVELOPMENT OF THE TREMATODA DIGENEA

PART I

THE BIOLOGY OF LEUCOCHLORIDIUM PARADOXUM

BY

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WITH 6 PLATES AND 7 TEXTFIGURES

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Preface.

Originally it was my intention to publish the first part only of this paper, my contributions to the biology of *Leucochloridium*.

As early as 1900—1908, while studying the plancton of the Danish freshwaters, I had observed that cercaria played a very prominent rôle in the plancton of our ponds and lakes. Being much occupied with other studies, however, I could not spare the time to undertake investigations on this interesting subject.

After an application from me in 1930 The Carlsberg Foundation purchased a house at Hillerød and equipped it as a laboratory for experimental studies relating to freshwater organisms. This laboratory is provided with numerous aquaria having air supply, thermostats at different constant temperatures, a very fine photographic outfit and a chemical balance. It is well supplied with the best microscopes and all the necessary instruments for limnological studies. It also contains a large library. On a site 2 km distant there are about 30 cemented open air aquaria. Owing to this magnificent grant it is now possible to keep cercaria-infected molluscs for months in the aquaria, to accelerate or retard the development of the parasites, and to transfer them experimentally to fishes and frogs. These excellent conditions for the study of freshwater organisms have revived my old interest in the biology of the development of the Trematoda, and I hope to be able to add a second part to the present paper later on.

It is my pleasant duty to tender my respectful thanks to the Trustees of the Carlsberg Foundation who, from the very beginning, have with the greatest generosity subsidised the investigations of our freshwaters. By this new great grant, left entirely at the disposal of the study of our freshwaters and freshwater-organisms, they have enabled us to extend our investigations to fields which have hitherto, in our country, been very little studied.

The author.

Hillerød, 20. Oktober 1931.

Chapter I.

Observations in Nature and in the Laboratory.

During my excursions along the rivulets and borders of our lakes I have very often found *Succinea putris*, which is very common in all localities of this kind. Where the snails have been abundant I have almost always gathered some hundreds of them, wishing to find the parasite *Leucochloridium paradoxum* which is now and then found in our country, but always only in a very limited number.

At last, at the borders of Tjustrup Lake in the middle of Seeland, only about one kilometre from the summer laboratory for freshwater biological investigations, I had the good fortune to find a single individual in July 1926. During the years 1927 and 1928 *Leucochloridium* was the main object of my investigations.

Since Heckert, in his admirable paper of 1889, has given a full account of the historical development of our knowledge of this very peculiar organism, it would seem superfluous to do this once more; a very short account will suffice.

In an old engraving from Halle Carus (1835) found a figure of a *Succinea*, the antennae of which showed several vividly coloured *Leucochloridium* sacks.

Ahrends (1810, p. 292) and Ramdohr (1810, p. 295) found and described *Succinea* infested with *Leucochloridium*. Ramdohr regarded the organism as a worm, and the contents of the sacks as eggs. Carus (1835) gave the parasite its name; he saw that the great green sacks were connected with a "Convolut weisser, unregelmässig angeschwollener, mit ästigen Enden fest gewurzelter Röhren von verschiedener Grösse" (pag. 92) and that this envelope was lying in the liver. He further saw that trematodes were found in the sacks; still, he was inclined to regard the contents as eggs, and supposed that the eggs were developed in the forepart of the sacks. He regarded the parasite as a worm, but supposed that it was derived from a generatio æquivoca, owing to the power of the liver to produce maladies "infolge eines Übermasses bildender Kraft". — Steenstrup (1842, p. 56) regarded the whole organism as "Amme", denied an origin from generatio æquivoca, and maintained that the parasite took its origin from small oval vivid cilia-covered organisms living in the tentacles of *Succinea* and of a similar structure to *Opalina ranarum*. On this latter point Steenstrup was mistaken, the organisms which he saw being most probably really *Opalina*. In 1845, p. 479 Dujardin created the name sporocyst, the name always used afterwards for this stage in the developmental history of the Trematoda. Siebold (1853, p. 425) showed that the sporocyst is an organism sui generis, being in no direct connection with the snail; the contents of the sacks are not eggs but germ-spheres ("Keimkörper") later on developing into larvæ which in the fully developed stage resemble *D. holostomum*. He supposed that the final host was to be found among waders and swimming birds, especially *Rallus aquaticus.* Seeing that the distoms in the sacks are motionless, whereas the sacks themselves are very mobile and furthermore of a very vivid colour, he supposes that the main task of the sacks is to allure birds and cause them to swallow the snails.

ZELLER (1874, p. 564) showed that it is at all events not water birds alone which swallow the snails; he ascertained experimentally that songbirds such as *Erithacus rubecula, Fringilla spinus, Sylvia atricapilla, Motacilla flava* tear the sacks out of the tentacles and then swallow them. He further showed that the ripe cercaria in the snails, when it has arrived in the alimentary canal of the redbreast and other songbirds, in the course of six days there develops into *Distomum macrostomum;* ZELLER as well as later authors (LÜHE 1909, p. 145 a. o.) have not been able to distinguish the two species *D. holostomum* and *D. macrostomum* from each other, and *D. macrostomum* is now stated to be found in water birds (*Rallus aquaticus, Gallinula chloropus, Orthygometra porzana*) as well as in long series of songbirds.

In 1889 HECKERT found the miracidium and gave a long, very valuable series of observations relating to the growth of the sporocyst, the infection of birds etc. It was shown that it was only possible to infect young birds, not older ones, furthermore that eggs were found in the layer of urine surrounding the faeces about 14 days after the infection with *Leucochloridium* sacks. In the eggs were found the miracidium larvæ. Leaves with excrements of birds were then given to the snails, and ten to fifteen minutes later miracidia were found in the alimentary canal of the snail. Later on the sporocysts were observed in the liver; a sack takes about three months to become fully developed. Curiously enough LÜTKEN in his little known work: "Snyltelivet og Snyltedyrene" 1895, (p. 56), writes: „Smaller birds such as nightingales and other songbirds hatch only the largest sacks so that the smaller ones get the opportunity to reach maturity; larger birds such as *Rallus* swallow the whole snail." This may be right, but as far as I know the view is based more upon suppositions than upon observed facts.

It must further be added that the *Leucochloridium*-sacks observed by HECKERT and all other observers were of a green colour with the apex of the sacks vividly red. A single time HECKERT found a sack with brown pigment. This brown form was found again by MAGATH (1920) and described as a new species, *Leucochloridium problematicum.* Its hosts were *Planorbis trivolvis* and *Succinea retusa.* The pigment was said to be of a "deep golden red colour" (1920, p. 110). Later on (1922) brown sacks were again found in Switzerland by MÖNNIG who gives a very thorough description of the histological structure of the organism. According to MÖNNIG the colour of the band is brown. The figures (Pl. VII, Fig. A by MAGATH and Pl. I, Fig. 3, by MÖNNIG) show almost quite the same colour; that of MAGATH is only a little brighter. That of MAGATH is a young sack; that of MÖNNIG an old one. The name *Leucochloridium paradoxum* Carus could in reality only be given to the sporocyst, the only sporocyst, as far as I know, which has a special name. When MONTICELLI (1888) dissolved the old genus *Distomum* Retzius he created the new genus

Urogonimus for all those species whose genital porus was terminal; the name of the parasite was then *Urogonimus macrostomus*. The genus *Urogonimus* was admitted by Loos (1899) and others. In the following we will use the name *Leucochloridium macrostomum* for the ripe stage, the parasite being best known under this name throughout the zoological world. See also Witenberg (1926, p. 226). As we shall often return to the papers of Heckert and Mönnig, we will restrict ourselves to the short remark that none of these two authors has found in the sporocyst the slightest trace either of any excretory organ or of a nervous system. With regard to the histological structure of the sporocyst I refer the reader to the two last-named scientists.

a. Investigations in Nature.

In the outskirts of Suserup Forest, along the borders of Tjustrup Lake in Middle Seeland, the sloping sides of the shore are covered with a dense carpet of *Petasites*, the stalks of the leaves being almost of a man's height (Textfig. 1). Small rivulets run among the leaves. The locality is very moist; the ground is covered with stones; in the copse bordering the forest and in the *Scirpus-Phragmites* zone of the lake there nest and live many birds belonging to the genera *Sylvia*, *Turdus*, *Fringilla* and others. The leaves of the *Petasites* are covered with numerous excrements, surrounded by white urine. After a long period of drought the leaves often look white-spotted. Very many snails live on the plants; *Helices* and *Succinea putris* are abundant in the locality from May, when the leaves grow up, until the latter part of September when the withered leaves sink to the ground and cover the stony soil with decaying matter. A great many of the leaves are eaten by the snails, greater and smaller holes giving evidence of their activity. — *Succinea putris*, especially, is found in three age-classes in the latter half of August. One very small yellow one with the viscera shining through the shell, a middle sized one, and a very large one, the two last-named sizes being of a homogeneous colour, dark greyish, or reddish yellow. Later on in the year, but also especially in spring, only the two last-named classes exist. The first class comprises the young brood of the year; those of middle size are one year old, and the last class at all events two years old, and it may perhaps also include three year old snails. During the autumn a great many of these old snails die, and the middle sized class predominates. Eggs are laid twice a year in the latter part of May, and in the middle of July; a sharp limit between the two egg-laying periods does not exist. During the two periods snails in copula are found everywhere upon the leaves. It was rather peculiar to see the great difference in size of the paired specimens; very often snails which were only one year old paired with those which were at all events two years old.

In the first hours of the day when the dew was still lying on the leaves, the snails were found upon the upper side. Shortly after the sun had begun to fall on the leaves the snails slowly disappeared. Creeping over the edges of the leaves or very often, especially in autumn, through the holes made by the Helices feeding on them, they arrived on the under side and fastened themselves there. — In periods of drought they crept down along the stalks; in very long periods of drought they totally disappeared from the plants and were then only found beneath the stones on the ground. The greatest activity was always displayed on warm moist summer days with a continuous fine drizzling rain, and with a temperature of about twenty to twenty-two degrees. On such days the upper side of the leaves would carry 15 to 20 snails and often about 10 *Succinea;* and on such days there was an enormous perforation of the leaves. In the autumn, at temperatures about 12 degrees, the snails were also

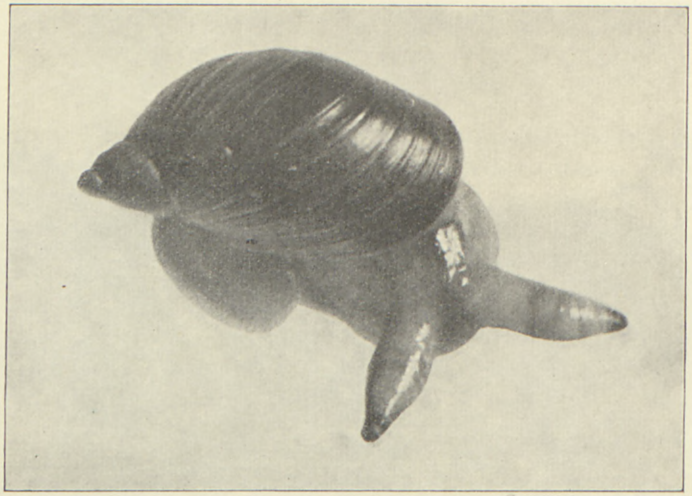
Textfig. 1.
The *Petasites* forest along the borders of Tjustrup Lake. (Berg phot.)

found upon the surface of the leaves on dark cloudy days but then they moved very slowly and mostly sat with the antennae drawn in. In stormy weather, even if it rained, and in thundershowers, no snails were found upon the upper surface.

Owing to the great leaves being commonly almost horizontal the excrements dropped by the birds, especially in the periods of drought, remained for weeks on the leaves. In rainy weather the excrements were washed off; most of the water followed the nerves of the leaves, reached the point where the stalk was fastened to the leaf and, following the stalk, finally reached the ground. Very often a little moisture was gathered round the attachment of the stalk; this moisture was very often of a greyish colour; in reality it was only the diluted excrements of birds. Just here, and in addition almost always on the excrements, snails could be observed eagerly sucking up the greyish fluid. *Limax, Helix arbustorum, Succinea putris* were here sitting side by side. The food material was the same for all the different species of snails, namely excrements, in which I several times found *Distomum* eggs, and in a few cases the distomes themselves; as far as hitherto known, only the *Succinea* are infested. Very often I have seen four *Succinea* sucking from the same excrements.

One day in July 1926, passing by the *Petasites* forest, I saw the first *Succinea* with a *Leucochloridium;* during the following three years I found about 150 specimens.

The locality was visited at all times during the period from May 1st to October 1st. During 1926 the *Succinea,* and especially those harbouring *Leucochloridia,* were only found in a very small part of the *Petasites* forest, that nearest to Suserup Forest, and



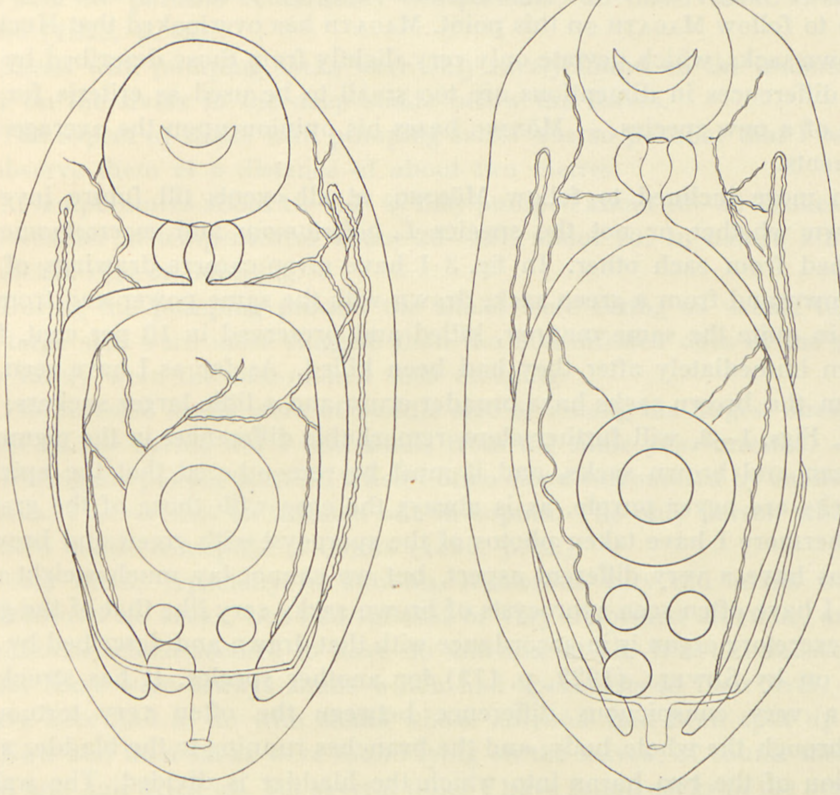
Textfig. 2.
A creeping *Succinea* with two pulsating sacks in the antenna. (Berg phot.)

where the beeches were hanging out over the *Petasites* leaves; the whole locality was most probably not more than about a few hundred square metres. During the two following years, and especially in 1928, the *Succinea* were found upon the whole of the *Petasites* forest, and those with *Leucochloridia* were also found there. The greatest number were, however, always found below or nearest to the beeches where the white spots of excrements were most abundant. During the years 1929 and 1930 the number of parasitised snails diminished.

As is well known, two forms of sacks, the green and the brown sacks, occur. In my locality I had, in 1927 and 1928, only found brown ones. In the beech forest itself near the borders of the lake, in a locality where small streams fall into the lake, the *Succinea* also occur. Very often I have searched for *Leucochloridium* here, but always without any luck. Then in August 1929 a single specimen was found, but this was green; later on in the same locality I found three other specimens, all green. In the main locality only the brown ones were found. It is rather peculiar that the two forms are restricted, each to its special locality.

Heckert has mainly found and worked with green sacks, Magath (1920) and later on Mönnig (1922) with brown ones. Heckert (1889, p. 14) found both brown and green sacks in the same snail. Most probably they belonged to two different sporocysts.

As far as I can see, the green sacks are a little more slender; the most conspicuous difference is that the green sacks have a red eye spot at the apex of the sacks, whereas the brown ones lack this. The pigment bands on the green sacks are



Textfig. 3.
Cercariæ from a brown and a green sack.

of a blue-green or dark blue-green colour, on the brown ones of a brown colour. There is very little difference to be found in the arrangement of the bands in the brown and the green sacks. As Mönnig (1922, p. 11) has observed, the rings in the brown sacks show a series of small elevations. In both cases the rings are most compact in the anterior part of the sacks and may here in old sacks be almost confluent, so that the whole anterior part almost looks brown; at the apex the rings may, as shown in the figure (Pl. I, Fig. 1) present themselves as a framework of small strings. No two sacks have the same arrangement of the rings. The older the sacks are, the more numerous, and more conspicuous are the rings. As mentioned above, Magath

(1920, p. 110) has tried to create a new species: *Leucochloridium problematicum* for the *Leucochloridium* with brown sacks. This *Leucochloridium* is said to differ from *Leucochloridium macrostomum* in the following points. 1) The sacks of *L. problematicum* are brown, those of *L. paradoxum* green with a red apex. 2) The lateral intestinal crura are 0.55 mm. in diameter in *L. problematicum*, in *paradoxum* they are much smaller. 3) The cercaria (= agamodistomum) of *L. problematicum* is larger than that of *L. paradoxum* (length 2.2 to 0.8 against 0.85 to 0.45). MÖNNIG (1922, p. 38) has not been able to follow MAGATH on this point. MAGATH has overlooked that HECKERT also found brown sacks, which deviate only very slightly from those described by MAGATH.

The differences in dimentions are too small to be used as criteria for the establishment of a new species. — MÖNNIG bases his opinion upon the average of twelve measurements.

I am more inclined to follow MÖNNIG, at all events till future investigations have shown whether or not the species *L. holostomum* and *macrostomum* can be distinguished from each other. In fig. 3 I have given camera drawings of cercariæ from a brown and from a green sack, drawn with the same power and from animals prepared in quite the same manner, killed and preserved in 10 per cent. formaline and drawn immediately after they had been killed. As far as I have seen, the cercariæ from the brown sacks have broader crura and a little larger suckers. A glance at Plate I, Figs. 1—2, will further show remarkable differences in the pigment bands of the green and brown sacks, and it must be remembered that the apices of the brown sacks are never purple, as is always the case with those of the green sacks.

Furthermore I have taken photos of the sporocyst with green and brown sacks. The photos have a very different aspect, but we cannot lay much weight upon this point, for I have often seen sporocysts of brown sacks very like that of the green one.

The excretory organ is in accordance with that drawn and described by HECKERT and later on by SEWELL (1922, p. 172) for another species. It has struck me that there is a very conspicuous difference between the often very tortuous canals running through the whole body, and the branches running to the bladder as a direct prolongation of the two horns into which the bladder is divided. The walls of the former have a glandular structure with very many nuclei; the others are quite straight, the walls are smooth, and no nuclei have been observed. I have not been able to see any pulsation in these rami (MAGATH 1920, p. 111). The flame cells are very difficult to see, and I have not ventured to draw them; HECKERT makes the same observation, and so does SEWELL with regard to *Leucochloridium assamense* (1922, p. 172).

After finding the first specimen, I gathered 500 snails from my locality and took them into the laboratory. The result was very meagre; not a single one showed *Leucochloridia* in the following days. During the first few days when the snails were examined in the locality, the result was the same; the weather was cloudy. On the other hand, on a rainy warm day I rather quickly gathered 13 infested specimens.

In the following I have collected my observations in nature of the infested specimens. The locality was visited 45 times, commonly for two or three hours every time.

1. It seems as if infested snails seek the light; they are very often seen balancing on the borders of the leaves, or sitting on the underside of the leaves with only the antennæ infested with the *Leucochloridium* protruding from the borders of the leaves; in this position, when the sacks are pumping with great regularity, the aspect is very peculiar, and the parasite remarkably conspicuous; an observation already made by MÖNNIG (1922, p. 49).

2. Snails with pumping sacks were only rarely found on the underside of the leaves, or on the stalks in the deep shade below the leaves.

3. The aspect of snails with pumping sacks was so peculiar that I was always able to observe them at a distance of about two metres.

4. At temperatures about 12—14° C. they pumped about 40—50 strokes a minute, in warm weather at temperatures about 20—22°, about 70. In nature I have never seen a quicker rate of pumping.

5. During the pumping process the snails were eating as usual; the infested snails of large size were more sluggish than the non-infested ones of the same size, and only rarely were the first-named seen creeping.

6. The infested snails were of middle size or among the largest ones, but only three times in late spring did I find snails from the same year infested.

7. During the pairing periods, when I often stood surrounded by snails in copula by hundreds, I never saw an infested one in copula. The only person who has ever seen infested snails in copula is CARUS (1835, p. 88).

8. Very often, especially in autumn, numerous very old snails were found which harboured no sacks, but had inflated or very deformed antennæ, and further some specimens which seemed to have no antennæ at all. It could subsequently be shown that these were always snails which had sporocysts in their liver. I suppose that I have here had to do with snails whose antennæ had been split up by birds.

9. Now and then sacks were found lying on the leaves; of course most of them were dead and half dried up, but several times I have found sacks in the act of pumping on the moist surface of *Petasites* leaves.

10. The eastern part of the *Petasites* forest was often mixed with *Glyceria spectabilis* and *Cyperaceæ*. Of course *Succinea* were also found here, and often in still greater number than on the *Petasites* leaves. Nevertheless I have never found infested snails upon them, I suppose mainly because excrements falling on these plants without horizontal surfaces are immediately washed away by the downpour, and do not lie for days upon the plants in a rather soft condition after the rain. In this connection it must be remembered that the parasitised snails are extremely sluggish in all their movements. If not disturbed, they most probably live on one single plant during a whole season, only moving from the leaf to its stalk and vice versa according to the moisture of the air. The probability of infection is therefore much greater on a *Petasites* plant than on grasses.

11. Curiously enough, however often I visited the locality, and though I often sat for hours in the vicinity, I never saw any bird sitting directly upon the leaves. Nor do I know why they should. Insect larvæ were hardly ever found on the leaves. Last autumn only, I found, in a very limited number, a small Lepidoptera larva, almost black with yellow rings. The birds were perched in the overhanging beeches and in the small alders. The redbreast, the blackbird, and the blackcap in the beeches, the wagtail at the borders of the lake, and the reed bunting in the *Phragmites* forest between the *Petasites* forest and the lake were the commonest. The excrements were dropped from the branches or when the birds were flying over the *Petasites* leaves. For my own part I could have snails with *Leucochloridia* before my eyes for hours. The birds were singing only a few metres from them, but nevertheless I never had the good fortune to see the birds take the parasites. I confess that this fact has always troubled me a good deal. For it must be kept in mind that hitherto no one has ever seen a bird in natural conditions attack a snail infested with *Leucochloridia,* nor pick out a sack from the antennæ. That the birds do so in captivity is not an absolute proof that they also do so regularly in nature. I have always thought that an observation of just this kind could not be said to be quite superfluous.

On the wall of my laboratory I had the nest of a redbreast, containing 6 young ones. As these left the nest, they began hopping round the garden walks searching for food. In the course of eight days I had made them so tame that they came on to the veranda of the laboratory and picked up crumbs of bread and insect larvæ thrown out only half a metre from my seat. I then covered my veranda with leaves of *Petasites,* and distributed six snails with *Leucochloridium* sacks, all pumping eagerly, over an area of one square metre. Some of the snails had one sack in each of the antennæ. To my eyes they were conspicuous at a distance of more than two metres. The redbreasts arrived as usual; three of them were hopping about the veranda simultaneously, and more than once I saw the birds sitting on the very leaf which carried the snails with pulsating sacks. Nevertheless they did not take the slightest notice of the sacks. I have repeated the experiment three times; the result was always the same.

Of course these observations are not in the slightest degree able to weaken the excellent studies by Zeller and Heckert. Nevertheless they have puzzled me a little, and I confess I have been sorry for all the wasted efforts of the sacks pumping and pumping at a rate of about 70 strokes a minute. It must, however, be admitted that my redbreasts were all young birds which had only left the nest a few days before. It is a reasonable conjecture, therefore, that the skill and attention of the old birds may be larger than that of the young ones. As shown in the following a large number of old snails possess old sacks shrivelled up behind the antennæ and without any pulsating power. This seems to show that at all events very many sacks never reach their destination.

12. It is difficult to say how great the infestation of the colony really was; at any rate it was not very great. Once my eye was adjusted to the object, I think that I soon discovered the infested snails available on that day; all infested snails were

commonly found during the first half hour of research, none later on. When it is borne in mind that I could often observe many hundred snails simultaneously, and that the greatest harvest of infested specimens on a single day was only 13, a one per cent. infestation would seem too high, one per mille probably being nearer the mark.

13. During the years 1927—1930 I gathered 500 snails every year, took them into the laboratory and there studied them for two or three days. Only one or two of these 500 snails were infested. After observation the snails were again placed on the *Petasites* leaves.

b. Investigations in the Laboratory.

All infested snails were taken into the laboratory; here they were isolated and given a substratum of leaves of different plants, *Petasites, Taraxacum, Circium* and others. A separate record was kept of each snail from day to day, from the moment of capture to the death of the snails. Some of the snails were under regular observation from June 15th to April 15th. As many as 25 cultures have been started simultaneously. Until November 1st the cultures were kept in my work-room, later on they were taken into a room which was never heated, and where the temperature oscillated between +2 to 8 degrees C. When the snails were dying, they were killed and conserved in formaline and sublimate. Very often they were taken at a moment when the snail was really dead, but the great sacks were still pumping behind the invaded antennæ.

Of course it would be too tedious to reprint all the 70 different records kept for a period of from one to ten months; but before trying to summarise the observations of the laboratory in a short sketch, it may perhaps be suitable to give a few of them.

No. 16 is a large snail, at all event two years old, most probably more. It was found on $^{12}/_{8}$ 27, having at that time two large sacks. It shows the sacks the following days, and the snail keeps on feeding the whole of August; nevertheless from $^{16}/_{8}$ sacks are never seen. On $^{16}/_{9}$ the snail fastens itself to the glass by a secretion, and is now fastened to the vessel till $^{17}/_{1}$. During the time $^{16}/_{8}$ to $^{16}/_{9}$ the snail is very sluggish, showing very deformed antennæ. On $^{17}/_{1}$ it is found creeping about slowly; the antennæ are thickened and deformed, quite as before the winter sleep. During the rest of January it creeps about slowly but takes very little food. Sacks are never seen. On $^{1}/_{2}$ it is again found agglutinated to the glass and remains there till $^{11}/_{2}$ when it dies. During half a year it has never shown sacks, but the antennæ have all the time been very deformed. The section shows two very large and very old brown sacks; they are quite motionless, and are infiltrated in the connective tissue of the snail from which they have been unable to liberate themselves. The sporocyst is very large and furnished with 5—6 smaller and greater sacks; the cercariæ are living and moving, both in the sporocyst itself and in the large sacks here surrounded by thick brown envelopes.

No. 22 is a large snail, at all events two years old. It was taken on $^{13}/_{8}$ 27, at that time showing two small sacks in the right antenna. On $^{27}/_{8}$ one of them is voluntarily thrown off; during the period $^{7}/_{9}$ to $^{7}/_{10}$ no sacks are observed, and on the latter date the snail is cementing itself to a stone. On $^{19}/_{3}$ I put the vessel in my laboratory (tp. 12—20° C.). On $^{22}/_{3}$ the snail is creeping about; the antennæ are as thick and irregular as on $^{7}/_{10}$. On $^{23}/_{3}$ two sacks are seen, one in each of the antennæ; they are very small and peculiarly acute. During the time $^{23}/_{3}$ to $^{25}/_{4}$ the snail feeds and makes large quantities of excrements. Simultaneously the sacks are uninterruptedly increasing in size and are extremely large in the latter part of April. From $^{20}/_{4}$ to $^{25}/_{4}$ the snail is sitting on the glass, it takes very little food during the last two days, the antennæ are withdrawn, and no sacks are seen; on $^{25}/_{4}$ it dies. During the period $^{25}/_{3}$ to $^{22}/_{4}$ the sacks are incessantly pumping, always with the same incredible force and regularity, c. 50—60 strokes a minute. We shall deal with this later on (p. 123).

No. 24 is a large snail, at all events about two years old. It was found on $^{15}/_{8}$ 27. The antennæ are deformed, but no sacks are observed. On $^{6}/_{9}$ it shows one in the right, and on $^{13}/_{9}$ one small one in the left antenna. During the time $^{13}/_{9}$ to $^{3}/_{10}$ it often shows sacks, now one in the right, now one in the left antenna; sometimes simultaneously one in each. During $^{7}/_{10}$ to $^{5}/_{1}$ the snail is agglutinated to a stone. From $^{5}/_{1}$ to $^{18}/_{1}$ it is mainly motionless but not agglutinated; it takes no food.

On $^{18}/_{1}$ it is dissected in the living state. It shows one very large sack and two smaller ones, absolutely motionless. A thin smaller sack shows feeble motion. The three sacks have all very long brown threads whose lumen seems quite obsolete; in addition there are a number of small sacks. All sacks show living cercariæ.

The two snails No. 16 and No. 24 have both very deformed antennæ which are by no means healed during the winter sleep. Nevertheless it seems as if the snails possess sight; they draw back the antennæ when arriving at objects about 1 or 2 mm. distant, and alter their direction.

No. 25 is a snail only one year old. It was found on $^{12}/_{9}$ and at that time had two thick very deformed antennæ. No sacks are seen. On $^{7}/_{10}$ the snail has agglutinated itself to the glass and has never shown any sacks all the time; it awakes from its winter sleep on $^{23}/_{1}$; no sacks. On $^{28}/_{1}$ it shows a small sack. On $^{28}/_{1}$ the snail is taken into a warm room; now it feeds and gives off many excrements. It is regularly fed and now shows two small sacks which grow steadily larger; they are rather large on $^{12}/_{2}$ and very large on $^{2}/_{3}$. Day after day the sacks are always pumping, always increasing in size, and the appetite of the snail is enormous. The rate of pumping is about 50—60 strokes a minute. On $^{15}/_{1}$ the snail has thrown off one of the sacks; it is still alive and lives for three days. On $^{18}/_{3}$ it dies.

No. 31 is a large specimen, at all events two years old. It was found on $^{12}/_{9}$ and had very thick deformed antennæ. No sacks are seen, and up to $^{12}/_{10}$ when the snail has cemented itself to a stone, it has never shown any sacks. On $^{4}/_{1}$ the snail wakes; the antennæ are as thick as on $^{12}/_{10}$, and immediately a small sack is seen pumping in the left antenna. On $^{19}/_{1}$ it is taken into the laboratory, the snail feeds vigorously; the sack is commonly withdrawn, but when exposed to strong light, the sack comes out but does not pump. Slowly the sack increases in size and from about $^{29}/_{1}$ it is always in the antenna and always pumping. On $^{6}/_{2}$ there are two sacks, one in each antenna, and almost of the same size. On $^{12}/_{2}$ both sacks are very large; on $^{13}/_{2}$ the snail throws off the one voluntarily, on $^{17}/_{2}$ the other; on $^{20}/_{2}$ the snail dies.

No. 32. The snail is large, at all events two years old. It was found on $^{12}/_{9}$ and had two thick very deformed antennæ, no sacks were seen. On $^{2}/_{10}$ it shows a very thin, very small sack in the left antenna. On $^{7}/_{10}$ the snail cements itself, sitting in the same place till $^{18}/_{2}$, then it creeps about till $^{28}/_{2}$. Food is offered but not taken. On $^{28}/_{2}$ it cements itself again, and dies about $^{20}/_{3}$, during the winter sleep. The antennæ have always been very deformed, but except during the days about $^{2}/_{10}$ the snail has never shown any sacks.

No. 42 shows quite the same course of life, but the snail is very small, only one year old, and it is perhaps questionable if it is not from the same year. It was found on $^{12}/_{9}$; it has thick deformed antennæ and has never shown sacks; it cements itself on $^{15}/_{10}$ and sleeps till $^{19}/_{2}$. Then it creeps slowly about or is out of the shell till $^{28}/_{2}$ when it cements itself again; about $^{20}/_{3}$ it dies during sleep.

No. 49 is a large snail, at all events two years old. It was found on $^{12}/_{9}$, and had thick deformed antennæ. Sacks are never seen; it cements itself on $^{15}/_{10}$, and now sleeps till $^{4}/_{1}$. It creeps about slowly and on $^{5}/_{1}$ shows a very small, very thin sack in the left antenna. It refuses to eat and dies on $^{19}/_{1}$.

In the following we will try to combine the different observations derived from studies in the laboratory; all accounts relate to infested snails.

1. With regard to the snails it may be said that from the middle of June till the middle of September they feed vigorously on the leaves of *Taraxacum, Petasites,* lettuce which are laid before them. This is especially the case with the young ones; the old parasitised snails are more sluggish. The leaves may be moist, but not excessively so; if the snails lie in water at the bottom of the vessel, they swell and will very often die. In the middle of September they are very sluggish, cease to eat, and commonly remain in the same place with the antennæ retracted, and half withdrawn into the shell. In the first part of October they cement themselves to stones or to the sides of the vessel. In the room where temperatures below $+5°$ have most probably never been reached, they often break off the winter sleep in the first part of January. If then taken into a warm room, they immediately begin to feed and may be as lively as in summer. When taken back to rooms with a temperature of about five degrees Celsius, they do not eat and again go into their winter sleep, which is not broken before the middle of April. Old dying snails usually sit several days with the antennæ withdrawn; they take no food at all. If laid with the shell mouth upwards, they are not able to turn round. The borders of the foot get blackish and crenelated; for some hours the snail still reacts to pricking with a needle; then it dies. Snails from the year before, or which are one year old, hibernate very easily in terraria, even if they harbour *Leucochloridia,* whereas the largest sized very often die during the winter sleep. Many infested snails die before the winter sleep, commonly as soon as they cease to eat. Only the peculiar antennæ show that the snails are infested.

2. Snails, especially those of the largest size, are able to exist with *Leucochloridia* for even a very long time without ever showing sacks in the antennæ; old snails have been kept for more than 6 months, and have never shown sacks during a dry period, i.e. in the period in which the snail has taken no food. The very long time the snail may exist with the parasite is rather remarkable. It has been maintained by many authors that infested snails die in captivity much earlier than non-infested ones (SEWELL 1922, p. 16, and others). This is often in accordance with my own observations, but on the other hand, I have had snails infested with the *Leucochloridia* more than a year, and am, therefore, inclined to suppose that a great number of snails which have once been parasitised carry the parasite during the whole of their existence, and that their lives are not much curtailed on that account. That the snails may in some cases get rid of the parasite and, as far as I can see, recover, is a fact which will be dealt with later on.

3. The abnormal structure of the antennæ almost always shows if the snail is infested. MÖNNIG (1922, p. 48) says: "Nach der Ueberwinterung sind die Schneckenfühler ganz normal.... Nach der Entfernung der Schläuche, wenn die Regeneration der neuen etwas lange dauern, geht der Fühler auch wieder in seinen normalen Zustand zurück." On this point my observations are not in accordance with MÖNNIG's. As far as I have seen, especially old snails never get normal antennæ again; those of the young ones always remain a little inflated. In very many cases I have observed and gathered snails in nature which did not show sacks in the antennæ; they were only abnormal. When taken into the laboratory, they would never show sacks for weeks or months, but when dissected, it could be shown that they were in reality largely infested with them. Old snails are very often found which either seem totally to lack every trace of the antennæ or in which the antennæ are only present as very small knobs. This may be due to the fact that birds have taken the sacks and injured the antennæ, but it is beyond doubt that snails which show thick antennæ before the winter sleep in October, and show no sacks before April, have the same thick antennæ in spring when they awake. Furthermore, sacks may be taken out of the antennæ, but even if the snail lives a whole year after, the antennæ will always be abnormal. In many snails the antennæ seem almost normal. A closer examination will, however, show that the one antenna is a little inflated and slight transparent. This is especially the case with young snails of very small size, and originating from the same year. If these specimens are taken into the laboratory, they may be kept for weeks before the very thin extremely acute sacks appear for the first time. Sometimes I have thought that an inflation of the antennæ precedes the intrusion of the sacks, but of course it is impossible to say if the sack has not in reality forced its way into the antenna at an earlier stage.

4. With regard to the nourishment of the sacks, the following observations may be made.

From $^{20}/_{6}$ to $^{15}/_{7}$ a snail had had a very large sack in the left antenna. It was taken into absolute darkness on $^{15}/_{7}$ and was kept there till $^{5}/_{8}$. Slowly the water in the vessel dried up and the snail agglutinated itself to the vessel. Brought into the light on $^{5}/_{8}$ the vessel was furnished with wet leaves of *Taraxacum*, and the snail came out in the course of half an hour and began to eat. Only five minutes later the sack appeared, but curiously enough it could now be shown that the sack was only half its former size. Killed and dissected, the snail showed only one ripe sack, so that there could be no doubt that it was the very same sack which had diminished in size.

It has been observed several times that snails which have thrown off their sacks and have had none for months suddenly show a long, slender, very acute sack in one of the antennæ. This is for instance the case with No. 25 which had never shown sacks from $^{12}/_{9}$ to $^{28}/_{1}$, furthermore with No. 31 with which the same was the case from $^{12}/_{9}$ to $^{11}/_{1}$. Both snails suddenly showed very thin, acute sacks, the one on $^{28}/_{1}$, the other on $^{11}/_{1}$. Both snails then fed vigorously and during the time from $^{29}/_{1}$ to $^{15}/_{2}$ and from $^{11}/_{1}$ to $^{30}/_{2}$ the sacks increased enormously. The same observation was made in the case of a snail in March—April (Pl. III, figs. 6—7). Figs. 22 and 25 show a snail, drawn with the camera on $^{23}/_{3}$ 27 and on $^{7}/_{4}$ 27.

That the very thin-walled central parts of the sporocyst creeping over the surface of the liver is nourished endosmotically by means of the fluids of the snail through the body-wall is of course beyond doubt. On the other hand it is not easy to understand how the old sacks are nourished. The above-mentioned observations show that the development of the sacks is dependent upon the health and strength of the snail. If the snail gets no food, the ripe sacks diminish in size, if the snail feeds vigorously, the sacks increase enormously in size. These fully developed brown-ringed strongly pulsating sacks never, however, have their place in the liver; they lie free of all organs in the body-cavity behind the antennæ, and can get no other fluids than those which are found in it. The walls of the sack are much thicker than those of the central parts of the sporocyst and, especially in old ones, brown and of a leathery consistence. As long as the sacks lie pulsating in the enormously distended antennæ, it seems rather improbable that they can get nourishment through the walls, whereas this may be the case when they are withdrawn and lie right behind the antennæ. — From a certain period in the life of the sacks, which may unquestionably be extended over months, nutriment from the mother sporocyst owing to nutritive fluid flowing from behind into the sacks through the stalks may be regarded as out of the question. The stalks turn brown, lose their lumen and brown cercariæ with very thick walls are often found attached, stopped in their wandering from the central part of the sporocyst into the sacks. In the life of the sacks a moment will come when the permeability of the walls being diminished, the pulsating power diminishes simultaneously, the turgidity also, and the result is the rather flabby, very brown sacks, often kneed, lying behind the antennæ.

When the snail has been withdrawn for some time and again begins to creep about, the sacks can be seen below the skin, dorsally, behind the antennæ. We then see the sacks pumping themselves into the antennæ, which are often distended to an almost incredible extent, being in some cases almost as long as the snail itself.

5. If there is only one sack, it is the left antenna which is most commonly infested; this is quite intelligible because the opening for the sexual organs is on the right side, and the large penis, the spermatheca and the albumen gland mainly fill out the right side of the visceral cavity of the snail. If the snail has two sacks, it very often creeps about with one in each of the antennæ, but often only one is out; the other lies within. In very old snails with very deformed antennæ large sacks are often seen lying behind the antennæ; nevertheless the sacks are never seen in the antennæ. Dissection shows that they have become enveloped in the tissues of the snail, or are lying twisted round the rudimentary penis, having got a kneed form with the knee lying just between the opening for the antennæ (Pl. IV, Fig. 1). It may very often be observed how two or more sacks, lying behind the opening for the antennæ, compete with each other; when one of the sacks has been pushed out into the antenna, another may be found lying in the posterior third of it.

6. When the snail dies, the sacks still keep moving, but always very slowly; it is especially the tip of the sack which preserves its feeling motion. When the putrefaction of the snail begins, the large old sacks keep intact for some time in spite of the destructive forces, and keep the cercariæ alive, the other parts of the sporocyst decompose and give off their cercariæ which are either lying in their cysts or creeping about freely in the dissolved viscera of the snail.

7. If one of the antennæ is cut off just at the moment when it is stretched out, still without showing any sack, the sack is not, as might have been expected, thrown off through the wound. The snail of course reacts by a violent contraction, and remains in the shell a few days; the two sacks now both go to the remaining left antenna, commonly lying behind each other.

8. As already observed, in natural conditions the large sacks are often thrown off almost voluntarily by the snail. Owing to the enormous distension of the antennæ and their viscous surface the slightest contact causes the skin to burst. Suddenly the sack lies pulsating on the substratum, at the same time, so to speak, tethering the snail. Immediately after the expulsion the snail draws in its antennæ and will now sit for hours, sometimes for days, half withdrawn in its shell without eating. I have seen 5 sacks thrown out voluntarily one after the other, all connected with the sporocyst within (Plate III, Fig. 8), and all in lively pulsation.

9. There still remains a fact to which I wish to draw attention and which has puzzled me a good deal for rather a long time.

On dissecting a number of snails parasitised by *Leucochloridia* we find in one snail only one, often enormous, sack, in another 6—8 sacks not so large, in a third perhaps no developed sacks at all, whereas the antennæ of the snail show that sacks have been developed. Why has one snail only one large sack, another 6—8 smaller ones? The snails may be of the same size. The transverse section in Plate VI will show why. Fig. 9 shows a transverse section of a snail not parasitised at all; to the right lies the very large liver, to the left the immense sperm-oviduct with a large albumen gland, and further the alimentary canal. The section in Fig. 10 shows a snail whose sporocyst carries one single enormous sack; the liver is much smaller and so also is the sperm-oviduct. Between the sack and the liver there lie a number of rings. These are transverse sections of a number of small sacks. At the very moment when the large sack is taken by a bird or voluntarily given off, an enormous space in the middle of the body-cavity will be empty (Fig. 11) and the great number of small sacks will get room to develop. Instead of one large sack we then get 6—8 sacks almost of the same size (Fig. 12). The transverse sections are from snails which were first anæsthetised and later put into sublimate.

When a young snail is parasitised, the sporocyst at first only develops a single sack; if this is not taken by a bird, it may grow up to the above-named enormous size. If it is liberated in some way, the numerous compensation sacks will simultaneously be developed. If the first sack has been taken at a rather early stage, there is never very much room in the body-cavity, and only a fewer number of sacks will then simultaneously reach full size. Sporocysts which carry 6—8 sacks, almost always carry in their central parts one or two short, very brown stalks with a rather sharply cut off terminal face; it is the rest of the thread which has carried one of these sacks formerly thrown off or taken by a bird.

Heckert (1889, p. 51) maintains that small snails carry small sacks, larger ones large sacks. This is not quite in accordance with my own observations; I have several times found snails which were only about half a year old carrying a single enormous sack, and very large snails with small acute sacks. When, therefore, Heckert says that the correlation in the size of the parasite and the host confirms the fact often found in the animal kingdom that "die Grösse des Tieres in einer gewissen Correlation steht zu der Ausdehnung seines Wohnortes" I do not think this interpretation is correct in this case. In the first place the sack is not the whole parasite but only part of it, and a large sporocyst may just as well carry many small sacks as a small one may carry one large sack. The size of the sack is in the first place dependent upon how long the time is from the moment the pulsation begins to the moment when it is taken by a bird.

10. The pulsation of the sacks is quite correctly described by Heckert and Mönnig. Heckert (1889, p. 15) says "Ist der Schlauch jung, so zeigt er eine von der Spitze nach der Basis sich fortpflanzende peristaltische, ist er älter, eine rhytmische Bewegung. Diese besteht in einem in regelmässigen Zeitabschnitten wiederkehrenden Zusammenziehen und Wiederausdehnen so dass man das Ganze mit einem Pulsieren vergleichen kann. Dasselbe findet eigentlich nur in der Gegend der beiden vorderen, dunkel gefärbten Ringe statt."

Mönnig (1922, p. 50) says: "In jungen Schläuchen bei denen Pigment eben erscheint, tritt die Pulsation in Form unregelmässiger peristaltischer Kontraktionen auf, welche von der Schlauchspitze nach hinten verlaufen. Sobald das Pigment weiter ausgebildet ist, ändert sich der Pulsationsmodus in eine rhytmische Kontraktion, welche hauptsächlich am stark pigmentierten vorderen Schlauchabschnitt stattfindet, wobei der Inhalt im hinteren Teil zurückgedrängt wird. Dieser Pulsationsmodus ist vielleicht besser geeignet das Eindringen in den Schneckenfühler zu ermöglichen."

As far as I can see, we have neither any real understanding of the physiological processes according to which the pulsation of the sacks takes place nor of their significance for the organism. What I can add to the understanding of these difficult matters is but little, a combined cytological and physiological investigation is greatly needed.

That light, as mentioned above, is essential for the pulsation is a fact beyond doubt which has been corroborated by all earlier authors. It ceases in total darkness. In accordance herewith we rarely in natural conditions find sacks in the antennæ of snails sitting below the *Petasites* leaves or on their stalks. Bad light conditions not only stop the pulsation but also often, though not always, cause the withdrawal of the sacks from the antennæ. On the other hand, if there is sufficient food and if the degree of humidity is great, darkness does not cause the withdrawal of the snail itself, at all events not during summer. This shows that the two organisms, the host and the parasite, at all events with regard to environmental conditions, are not fully adapted to each other.

However, whereas the pulsation is conditioned by light, it is the temperature which determines the rate of pulsation; as mentioned above, in nature it may range from about 40 to about 75 times a minute, in the laboratory much greater oscillations may be observed. In vessels with great humidity and high temperatures (about 30° C.), which are standing in the sun, the pulsation may rise to 120 to 125 a minute. When autumn comes, only 30 pulsations a minute are observed, and likewise during winter at temperatures of 4—6° C. When the snails awake now and then during the winter sleep, the pulsations are extremely slow, not more than 2 to 5 a minute.

The activity of the sacks is enormous, especially in the summer months and in humid air. I have had snails, which, as far as I could see, had pulsating sacks uninterruptedly for weeks. They pulsated at $10^1/_2$ in the evening, at 1 o'clock at night, and at 4 o'clock in the morning; when observed again, they were still pulsating. In our luminous summer nights it is highly probable that the pulsations go on without interruption. In nature pulsation is unquestionably dependent on climatic conditions. Thus in periods of drought the pulsation may cease for weeks during the day, and in warm humid periods it may never cease.

From a physiological point of view the sacks, as far as I can see, are some of the most peculiar bodies in the whole animal kingdom. This is also the view of HEMPELMANN (1926, p. 152). For it must be remembered that in the *Leucochloridium* we are concerned with an organism in which we have never found either the slightest trace of a nervous system or a blood system, nor any sensitive organs of any kind.

From this very organism, which always lies motionless in the interior of the snail, parts are developed (the sacks) connected with it by means of long thin threads, the lumen of which seems to be obliterated, and whose skin, especially in old specimens, seems so thick that its permeability to nutritive juices from the host seems rather problematic. These very same sacks, in contradistinction to the other part of the sporocyst, though quite like it without any trace of a nervous system or sensitive organs, react very considerably to influences from without such as light, temperature and humidity. To some degree their expressions of life are dependent upon those of the snail. When the snail is withdrawn in its shell, the sacks are forced to keep quiet; they must sleep their winter sleep when the snail does so. And when the snail has cemented itself to a stone in a period of drought, there is no possibility of motion. On the other hand, the snail may creep about for weeks, eagerly taking food; nevertheless, even if the snail lives an active life, the sacks may be observed to keep quiet behind the antennæ, now and then slowly pulsating, and then they may suddenly push forward into the antennæ and pulsate daily for weeks. As far as I know, we know of no other organism which is able to produce parts of itself without sensitive organs or a nervous system of any kind which after a resting period of months, as soon as light strikes them, are suddenly able to react in the course of a few minutes, producing effects which it is not in the power of the other part of the organism to produce. In this connection it must, however, be remembered that in the miracidium stage of the trematode as well as in the cercaria stage we find a well developed nervous system as well as sensitive organs; the sporocyst may be regarded as the metamorphosed miracidium. Even if we have not found any trace of a nervous system in the miracidium of *Leucochloridium*, it seems to me rather problematic to deny any trace of a nervous system in the sporocyst, especially because we know that in the agamodistom stage and the ripe trematode it is as well developed as in other trematodes. Furthermore Loos (1900, p. 212) found a nervous system in sporocysts of other trematodes, even if it was of a very simple type.

It is Loos (1892, p. 166) who has advanced the opinion that the differences between the miracidium, sporocyst and redia are all nothing but gradations. They are homologous; in all stages the same plan of structure is found. This view has been further developed by Sewell (1922). At p. 301 he says: "In fact we can quite easily form a graded series. Commencing at one end with an undoubted sporocyst, which appears to be devoid of all structure, and passing through forms in which certain organs are partly developed and which might be considered to be either sporocysts or rediæ, we get, at the other extreme "rediæ" with a highly developed alimentary canal, a complicated excretory system, definite nervous system and genital organs, and active locomotor processes." A sharp division between sporocysts and rediæ cannot be made. "They are homologous stages in a line of parthenogenetic development, in which the process of degeneration has proceeded to a varying extent." I suppose Sewell is right when he says that the greater our knowledge regarding the various forms, the more certain it appears that no hard and fast boundary can be drawn between them.

It is of course very strange that such skilled observers as Heckert and Mönnig have not been able to find the slightest trace of a nervous system. Nevertheless with the above-named view in mind it will be understood that it will not be correct to deny nervous elements even in the sporocyst of the *Leucochloridium*, even if a nervous system has not been found.

As mentioned above, what we know and are able to show experimentally is that light is essential for the pulsations, furthermore that their number depends upon the temperature. How these outer stimuli cause locomotion of the sacks, we do not know. As is well known, the heart muscle of a developing chicken when it has no nerve-cells at all, is, like the sacks, able to perform rhythmical contractions (Starling 1920, p. 985). On the other hand there is this great difference between the sacks and the heart, that the sack may be set out of motion regularly during the night, during drought and for months in hibernating periods, and nevertheless in the course of a few hours, or perhaps in a still shorter time dependent upon the activity of the snail, be capable of renewed rhythmical motion.

Also in the mode of reaction to external stimuli, especially light, the above-named heart and the sack differ very much, a certain power of light being a condition sine qua non for the pulsation of the sack whereas the heart is quite independent of this factor.

How independent the movement of a sack is of the mother sporocyst, and how much it depends upon light is best shown in the following manner. If a sack as soon as it is thrown out of a snail is put into a physiological NaCl solution and placed in diffuse daylight, it may live there for three days. During the first day it will pulsate slower and slower; during the following two days it will keep quiet, but if pricked with a needle it will react. The first day it will further be seen how the sack, pulsating steadily, is revolving round its own axis, and in this way rolls from one side of the vessel to the other. On the other hand, if the vessel is put in the dark no motion of any kind is observed. This shows as plainly as possible that the primus motor of the motion is the light. Pl. II, Fig. 3a—e shows the same sack drawn with the camera and in the course of 10 minutes. The figures illustrate how extremely variable in form the sack is, and that the greatest form variations take place in the anterior part of the sack. Fig. 3f is the same sack killed in formalin.

The pigment in the sporocyst of *Leucochloridium* is in itself a very peculiar thing. Only very few pigmented sporocysts are known (*Cercaria cotylura* (Pagenstecker 1863), *Cercaria cystophora* (Wagener 1866, p. 145), sporocysts of *Gasterostomum* and *Echinostomum* (Haswell 1903, p. 279)), but in none of these cases is the pigment restricted to special parts of the sporocyst, and we do not know anything with regard to its significance.

Mönnig has supposed that the strong development of pigment in the ripe sacks which alone have the power of pulsation, and the absence of it in the young ones which do not possess this power, makes it probable that it is really this pigment which may in some way be able to transfer stimuli from the light to the organism, and then cause the rhythmical contractions of the muscular system.

Furthermore Mönnig (1922, p. 19) has found in the sacks a myoblast syncytium which he describes in the following manner. "Dieses Syncytium setzt sich aus grösseren kernhaltigen Partien, die zuweilen bis fünf Kerne enthalten, und die mit einander durch kernlose Protoplasmastränge verbunden sind, zusammen.. Es herrscht hier also kein Monopol eines Myoblasten über seine Fasern; alles ist mit einander verbunden und dadurch sind auch die Faser selber alle mechanisch mit einander in Kontakt gebracht. Ob dieses aussergewöhnliche System vielleicht mit der merkwürdigen Pulsationfähigkeit der Schläuche zusammenhängt, indem die Reize durch das Myoblastemsyncytium geleitet werden, ist schwer zu sagen." From these observations it may provisionally be permissible to suppose that light in some way acts as a stimulus upon the pigment, from which it is transferred to the muscles. How the stimulus is conducted to the muscle systems, the myoblast muscles, the longitudinal, and ring muscle layer, and how they interact is an open question; it need only be added that in the sacks we find that the muscles have a spiral striation not commonly found in the Trematoda, and here in *Leucochloridium* most probably connected with the enormous amount of work demanded by the sacks.

11. If it is difficult to understand the real manner in which the pulsations take place, it is not much easier to understand the purpose of the motions. As far as I can see the purpose is threefold: a. They cause the intrusion in the antennæ of the snail; b. they pump the cercariæ out of the sacks; c. they allure the birds.

a. When infested snails are kept in darkness and then suddenly exposed to the light, they will begin to creep. It may then be seen that the sacks behind the antennæ begin to pump, whereupon they commonly glide into the antennæ; this always takes place when the snail is fully stretched out. As far as I can see, the intrusion in the antennæ is dependent partly upon a certain pressure in the body cavity of the snail, partly upon the pulsations which may perhaps help a little, especially owing to the ring walls in the forepart of the sacks which to some extent act like the well-known ring walls in woodboring larvæ (*Cerambycidae* etc.). But the motion in the snail is also dependent upon the pressure in the sack itself. If a sack is punctured with a needle, it will very soon from a stiffened body be altered into a flabby one. It will behave like a caterpillar which has been pricked. The turgescence is of the greatest significance for the motion. In very old brown sacks this turgescence is lost; the pulsations are very small and the sacks lose their power of forcing their way forward. They then lie behind the antennæ and are often handicapped by younger ones which push past them. The old ones are then very often entangled in the tissues, are kneed, or get very irregular forms. They are loaded with agamodistomes mainly deposited in the posterior part, which is much the broadest; anteriorly they are provided with a small sharply marked almost black part which only possesses slight power of pulsation, whereas the posterior part is quite motionless.

b. More than once I have observed a peculiar phenomenon in the pricked sacks. The pricked sacks continue the pulsations for some minutes. For every pulsation an agamodistome is pumped out of the little hole. The result is that the mass of agamodistomes lie like a milky cloud round the hole. The pulsation of the sacks may perhaps have a secondary purpose, that of pumping the cercariæ out of the sack. For it must be remembered that the sack is most probably swallowed whole, either by the mother bird or by the nestlings, to whom it is brought in the beak of the mother. The walls of the sacks are very solid, we suppose that the gastric juice of the mother bird is not sufficient to dissolve the cysts of the cercariæ, but as far as I know, no one has taken into consideration the fact that in many cases it is the sack itself which must be dissolved before the cysts surrounding the cercariæ can be dissolved. When almost all the cercariæ are pumped out, the flabby sack lies motionless. I have preserved such sacks, with their gathering of cercariæ lying in a clump round the little invisible wound.

c. According to the common opinion the main purpose of the sacks is to draw the attention of birds to the parasitised snail, and so cause the bird to split the antennæ of the snail and fly away with the sack. This would demand an almost incredible power of adaptation on the part of the parasite. We shall return to this point later on.

12. With regard to the central parts of the sporocyst[1]) a few remarks would seem appropriate. The methods employed were the following. In many cases the snails were vivisected. In this way it is possible to see the young distoms through the skin of the young sacks before encystation, and to follow their wanderings into the sacks. In most of the cases the snails were narcotised by means of chloral and when fully narcotisised drenched with warm sublimate formaline. Then the shell was broken off, and the mantle cavity opened. In this way it was possible to study the whole sporocyst lying in its quite natural position often with the sacks halfway out in the antennæ.

The parasite is in the first place a typical liver parasite, nourished by this organ. As far as my experience goes, the sporocyst always lies in the same place in the second winding, covering the surface of the liver. As soon as the shell is broken off, the white sporocyst is seen shining through the skin. Its threads may come near the hermaphrodite gland, but they only rarely enter into it and have no direct contact with the sperm-oviduct. On opening living snails, a bunch of long threads are seen floating in the body cavity (Plate VI, Fig. 8); on fixed material the sporocyst lies as a broad white comb pressed against the liver (Plate VI, Fig. 2). As a rule it is not in contact with the alimentary canal of the snail. Now and then two well separated sporocysts are found; this was already ascertained by Heckert and Mönnig. As it may be expected that the snail, when infested by eating the excrements of birds, or creeping over the place where egg-infested excrements have been thrown out, has got many eggs into its alimentary canal, it is rather peculiar that the actual number of sporocysts is almost always one, very rarely two, and, as far as is known, never more than that. Most probably this may be interpreted to mean that even among the parasites in the same host there is a struggle for existence, in other words, the specimen which has obtained the best place with regard to food supply and shelter will be victorious.

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[1]) I do not agree with Maggath (1920 p. 110) who uses the name sporocyst only for the sacks and describes the rest of the parasite as knob-like projections connected by thread-like processes. The whole organism may be designated as a sporocyst. The ripe sacks and the thread-like processes cannot be distinguished from each other, the first named are only a later stage in the development of the lastnamed.

Heckert (1889, p. 13) describes the sporocyst as a "Sporocystenfadenwerk" "eine mehr oder minder grosse Masse reich verzweigter Fäden, die wie die Äste eines Baumes von einem gemeinsamen Mittelpunkte aus ihren Ursprung nehmen und mit abgerundeten Spitzen endigen". Most of the other authors give the same description. Only Mönnig (1922, p. 9) deviates from this commonly accepted conception. He maintains that the sporocysts "zeigen immer einen deutlichen Zentralkörper und eine Anzahl davon abgehender Schläuche".. "Die Sporocyste setzt sich aus diesen beiden histologisch und funktionell von einander verschiedenen Teilen zusammen. Der Zentralkörper.. stellt die Keimstätte der Cerkarienbrut und sorgt auch für die Ernährung des ganzen Körpers. Die Schläuche sind secundäre Bildungen; aus ihrer Wandung habe ich nie Keimzellen hervorgehen sehen; sie dienen lediglich zur Verbreitung der Brut." I must confess that the description of Heckert and others is much more in accordance with my own observations than that of Mönnig. Notably I may maintain that I have never seen a sporocyst of the form which Mönnig figures in Fig. 1, Plate I. Only in very old, almost dying, sporocysts may sacks be found of the form which Mönnig has drawn. (See also Textfigs. 4 and 5).

There is a great difference between the very young just ramified sporocyst and the very old ones, whose power of reproduction is almost exhausted (Plate II, Fig. 1). It is almost impossible to see with certainty whether or not a snail which has never shown sacks, and whose antennæ are normal, is infested. After vivisecting 25 specimens I had the good luck in two snails of very small size to find two whitish spots on the surface of the liver; they were sporocysts whose threads were only 1—2 mm. None of them contained ripe cercariæ, and the whole sporocyst was only about one sq. mm. They were found on $^{4}/_{9}$; as the time used for the full development of the sporocyst is maintained by Heckert to be about three months, this is in very good accordance with the supposition that the snail has emerged from the egg in the first part of June, and has most probably become infested in the first part of July. At all events, in these young sporocysts a "Centralkörper" is not separated as a special part from the sacks. The threads carry branches of the second order; these are always very short.

The sporocysts of very old and very large snails which have been infested perhaps for years, differ very much from those just described (Pl. II, Fig. 2). There are extremely few ramifications; the formation of sacks has ceased; from the large, very little ramified, central part there issue only a few long white sacks like threads, often of the same breadth at the base and the apex. These are sacks arrested in their development. Furthermore there are some brown very short knotty threads (Fig. 2) which at an earlier period have borne sacks and others still bearing a few very dark sacks, without the power of pulsation. The formation of germ-spheres has ceased. In the central part of the sporocyst there occur only a very few cercariæ (agamodistomes); in the long white threads hardly any; in the old sacks they are, however, numerous. Their envelopes are very thick and almost intransparent. Some of the old sacks are extremely irregular, containing very few agamodistomes; in these old sacks the agamodistomes are often arranged serially so that the sacks resemble a string of pearls (Pl. I, Figs. 3—4). The agamodistomes have here very thick walls, often so thick that they are quite opaque.

Between these two types of sporocysts, the very young ones and the very old

Textfig. 4.

Textfigs. 4—5. Two sporocysts with very young sacks and some free lying agamodistomes. (Berg phot.)

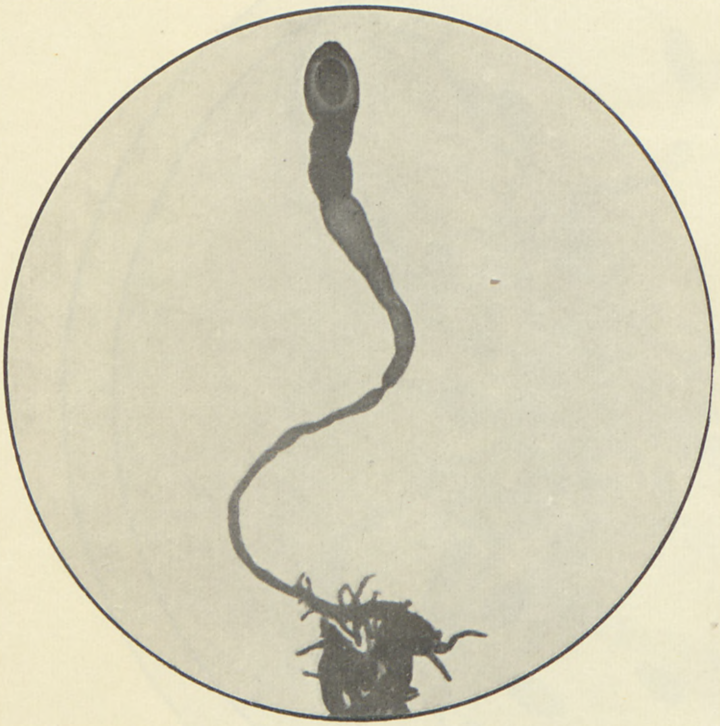
ones, there are all the intermediate stages, the strongly ramified sporocysts with 2—8 fully developed sacks, the long threads more or less altered into sacks, threads with branches of the second order, and threads without branches.

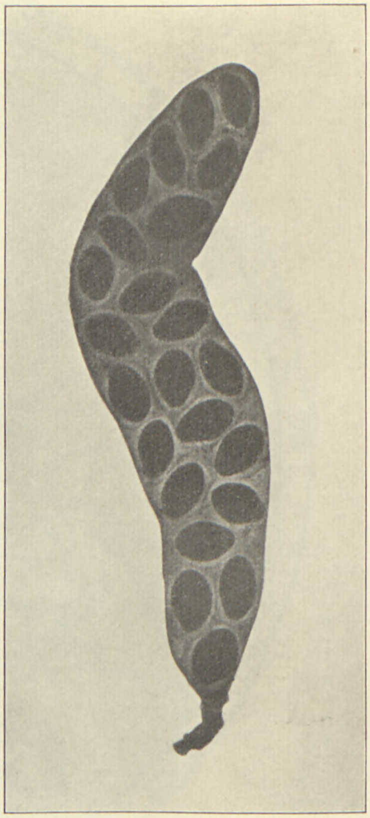
I will not venture to decide if the sharp distinction which Mönnig makes between the central body and the sacks is correct. In my specimens I have not been able to see it, at all events not in sporocysts with brown sacks. Nor do I consider his assertion correct that only the central body of the sporocyst is able to produce the cercaria-brood, whereas the sacks should only be of significance "zur Verbreitung der Brut". HECKERT also (pp. 18—20) has not maintained this very sharp distinction.

Textfig. 5.

In a sporocyst in full vigour and carrying 2—6 large pulsating sacks one will in its interior as well as in the numerous not fully developed sacks find germ spheres of all sizes, from very small globular bodies to almost fully developed agamodistomes. Only in the large pulsating sacks we find no germ spheres. When the sacks have reached the antennæ, the brown rings have become conspicuous and the musculature enormously developed, no germ spheres are developed, perhaps owing to lack of sufficient food as the permeability of the walls gets smaller.

In the ramified central parts of the sporocyst, and in the young slender sacks, fully developed agamodistomes, but without any conspicuous envelope, are found. They creep about rather briskly, bending and stretching the body in all directions, living in the serous fluid which fills the sack, and by which they are nourished. Many begin to wander out into all the club-shaped fully developed sacks. A single time,





Textfigs. 6—7.
Two sacks. Fig. 6 a very young one only containing a single agamodistome. Fig. 7 a much older one containing agamodistomes but still without bands and pulsating power. (Berg phot.)

when I had opened a living snail and immediately brought the sporocyst under the microscope, I found a long club-shaped sack with faint bands of pigment, a sharp distinction between the sack and the thread, and with slight pulsating power. The thread was filled with numerous wandering cercariæ which moved upwards into the sack. In the very narrow lumen of the thread the cercariæ were altered into extremely slender, threadlike bodies, 6 times longer than broad. They were gliding over each other and all in the same direction. Upon arrival in the sack itself the body was contracted and the length was then only about $1^1/_2$ times the breadth. — This enormous power of elongation and contraction of the body resembles what is known with regard to the rediæ.

Just like the rediæ, they are able to increase the length of the body very considerably and pass through very narrow strings and openings. Cort (1915, p. 23) says that the rediæ belonging to *Cercaria diastropha* may augment the length of the body 5—6 times; he (1915, p. 21) makes a similar observation with regard to *C. inhabilis.* The wandering cercariæ of *Leucochloridium* do not possess the locomotoric winglike processes characteristic of the rediæ, but on the long threadlike bodies which I saw wandering through the threads of the sacks I distinctly saw how the body on the side of the acetabulum was dilated to form conspicuous flaps which were again withdrawn. At first this observation troubled me a good deal; but a closer examination showed that the body near the acetabulum was always broadest, and that the forepart of the body, when it was lying still and the posterior part was drawn forwards, was pressed downwards and round the acetabulum, which gave it the appearance of winglike flaps.

Heckert has shown that at the bottom of the sack there is found a peculiar closing mechanism (Plate I, Fig. 5), preventing the agamodistomes from getting back into the lumen of the threads again during the pulsations. The closing mechanism consists of a large number of threads projecting from the inner side into the lumen of the sack and closing it behind. They may be found in every ripe sack; when they are formed, the peculiar sausage-shape of the sack is sharply marked off from the stalk.

In these fully developed sacks the agamodistomes may lie in so great a number that their envelopes become hexagonal owing to pressure (Pl. II, Fig. 4). The agamodistomes in a number of 100 to 200 are here always surrounded by their very thick cuticula; this cuticula derives from a double ecdysis. It remains with the larva, forming a protective covering round it. The suckers are connected with the cuticula and between it and the larva is a very transparent fluid. The large numbers of agamodistomes mentioned by Carus (300) (1835, p. 90) and others I have never observed (Heckert). The agamodistomes lie so closely packed together that there is hardly any space between them. They may lie there for months, perhaps for years, their membrane getting steadily thicker and more opaque.

As for the rediæ they do not always take food endosmotically; they are also able to take food through the mouth opening. Rossback (1906, p. 382) a. o. have seen the rediæ by means of the muscular pharynx nip off small portions of the "Keimkörper" lying in the interior of the sporocysts, as well as portions of the liver and other parts of the body of the snail. I have especially in many rediæ belonging to the echinostomes cercariæ found the long stomach filled with yellowish brown particles which can only belong to material nipped out of the liver. With these observations in mind I tried to discover whether the cercariæ, when creeping about in the interior of the sporocyst, would take food through the mouth opening i. e. swallow the "germ-spheres" which were lying free in the fluid. This has never been observed. It may be supposed that the serous fluid in the sporocyst, passing endosmotically from the snail into its interior, is either swallowed directly by the mouth opening or once again passes endosmotically through the skin of the cercariæ. When they are lying in the sporocyst enveloped in their thick walls, it is questionable if they get any food at all. The only sign of life is from the contractile vesicle, which is emptied at regular interrvals, in the summer several times a minute. In the threads of old sacks very opaque dark cercariæ are often found; the stalks are swollen before and behind them; they fill up the whole lumen, and hinder any new invasion of cercariæ into the sack. Simultaneously the threads get a brown knotted aspect. We are unquestionably right when, from a biological point of view, we compare the agamodistomes in the sacks with the encysted stages of other Trematoda. With regard to the envelope there is only the difference that, in the last-named case, it is formed of exudations from cystogeneous cells, while in *Leucochloridium* it is the skin itself.

14. It is a well-known fact that we possess a long series of investigations relating to the influence of the Trematoda upon snails. I here refer especially to the works of Faust (1920), Agersborg (1924), and Hurst (1927), and to the literature cited by these authors. All these investigations, however, never deal with *Leucochloridium*, and it is open to question whether the results gained from other Trematoda will also apply in the case of this parasite upon the snail.

In all the other cases the parasites either as sporocysts, as rediæ, as cercariæ or in incysted stages, may be distributed over the whole snail; as rediæ they are able to nip off parts of the tissue of the host; sporocysts do not take this nutriment. Many cercariæ, especially monostomes, are liberated from the sporocysts at a very early developmental stage. They are then nourished directly from the host, and live for weeks or perhaps more, free in the body-cavity and organs of the host. The *Leucochloridium*-sporocyst never invades the organs of the snail with thousands of parasites. The progeny is developed in its own interior and this progeny never comes out into the snail itself. It is the same single organism, the steadily growing miracidium, which from the first day of its life to the last nourishes the whole progeny, and the nourishment only takes place endosmotically. In its whole life *Leucochloridium* is a true liver parasite. From the liver it may send its sacks into the hermaphrodite gland and into the body-cavity, but as far as I have been able to see, the organs are not intervowen and filled with a parasitic mass as is the case with organs infested with developmental stages of other Trematoda.

A more elaborate study relating to the influence of *Leucochloridium* upon the tissues of the snail is still a desideratum. In spite of the fact that I possess many sections through parasitised and non-parasitised snails, I fear that my results have not sufficient validity, and I hope that others will take up the work that has been left undone. I only wish to call attention to a single point.

It has often been maintained that parasitised snails assume another colour, owing to parasitation, and that such snails may be distinguished by their colour. Thus Biehringer (1884, p. 1) says with regard to the large *Limnæa* that heavy infestations cause a peculiar yellowish white colour in the apex of the snail. According to my experience this is especially the case with snails strongly infested with *Tetracotyle*. Hurst (1927, p. 335) says that a dirty grayish colour with a more or less yellowish or orange shade in the region of the viscera is characteristic of parasitised snails, and maintains that healthy snails are usually much darker in colour than unhealthy ones. The change in colour is caused by a reduction of the pigment of the snail, and by the appearance of the pigment of the parasite itself.

As mentioned in my Furesø Studies (1917), one of the most characteristic snails is the very large *L. ovata* characterised by its bright yellow colour; black pigment spots in the skin shine through the shell. Among a large material dredged from five to six metres' depth I found a single very large snail which was of a very peculiar pitch-black colour. When the animal was taken out of the shell, it could be shown that it was the shell itself which was black, only the columella was a bright white. Also the animal itself was not yellow like most of the other specimens, but much darker. The animal was infested to a degree which I have never seen before. In reality it was almost only one enormous living mass of sporocysts, producing incredible numbers of Furcocercaria.

In the following months I saw that very many snails were black at the top of the shell. When the material was large, it was an easy matter to form a series of snails typically yellow at one end of the series and totally black at the other. When dissected, it was shown that the degree of parasitation was proportional to the melanisation of the snail itself and of the shell.

The same was the case with regard to the bright yellow *Bithynia* from the same locality, whereas the *Valvata*, also heavily infested with Furcocercaria, showed no conspicuous variations in colour. In the second part of this paper I shall return to the pelagic Furcocercaria-fauna af our lakes.

As far as I can see, the *Succinea*, even if heavily infested, show no conspicuous variations in colour. As is well known, the snail in itself is commonly dark, often black, whereas the shell has its well-known amber colour. Sections through the liver of parasitised snails show an enormous deposition of pigment, but the shell itself, even if the snail is heavily infested, is always a bright amber colour. Now and then, we find peculiar grey-coloured *Succinea*. I thought that this was perhaps the result of a parasitation, but sections showed that this was not the case.

In this connection it may perhaps be pointed out that the excreta of the progeny of *Leucochloridium* are never deposited in the host itself as often may be the case with other Trematoda. In *Leucochloridium* they are deposited in the mother sporocyst. Further investigations must show whether it is not these very same excreta which the sporocyst in any way uses to build up the bands of pigment in the ripe sacks, hitherto unknown among all other sporocysts.

15. During the sexual periods, when standing in the *Petasites* forest, I was often able to observe about 20 snails in copula. On rainy days copulating individuals could be found by the hundred. During the four years of my observations I have never seen copulating individuals carrying sacks in the antennæ. When kept in terraria, my snails very often laid eggs, but I never saw a single parasitised individual which had laid eggs. Curiously enough, Carus (1835, p. 88) maintains that he has

observed a parasitised egg-laying individual. From my own observations I supposed that *Leucochloridium* affected the snail sexually, and that in this as in so many other cases we have to do with a parasitic castration.

For the purpose of studying this phenomenon, snails, when dying, were given chloral, they were then put in sublimate and dissected. Later on they were opened and camera drawings were made, a series of camera drawings being often made during the dissection. The sexual organs were not touched until the whole sporocyst with all its sacks had been laid bare; they were then taken out and drawn by themselves. Several of the snails were studied for months while alive, and regular notes made every day.

Firstly a short description of the sexual organs of a non-infested snail must be given. The hermaphrodite gland is relatively large and almost black. The hermaphrodite duct is black or greyish, always very much twisted and only rarely provided with more than one black vesiculum seminalis; the male and the female part of the sperm-oviduct are always quite distinct. The female part of the sperm-oviduct is strongly folded and provided with an albumen gland whose size varies extremely according to the season of the year and the age of the individuals; the free part of the oviduct carries upon a stalk a globular spermatheca; the vas deferens is long and thin; where it reaches the penis is found a retractor which is commonly cleft into branches attached to the diaphragm. The penis itself is relatively long. Neither penis nor the free oviduct possesses appendages of any kind. Vagina is situated just above the opening for the male organ. The results of the sections will be given in the following.

Snail No. 2 (Plate IV, Fig. 6) was found on $^{25}/_{6}$ and on that day showed one large sack. On $^{16}/_{8}$ it shows two; the second one is rather small; on $^{6}/_{9}$ the second one has almost reached the size of the first; during the time from $^{16}/_{8}$ to $^{15}/_{9}$ it has every day shown one or two large pulsating sacks, often pulsating about 100 strokes a minute in bright sunshine; during the time from $^{15}/_{9}$ to $^{25}/_{9}$ the snail is often withdrawn, and even if the very deformed antennæ are out, it shows no sacks; it is very sluggish and will not take food. On $^{25}/_{9}$ it is narcotised and dissected. It shows two very large sacks of which especially the one is very large, curved and so placed that it has most probably been impossible for it to get out into the antennæ; the sporocyst has only produced these two sacks; the outer side of the liver is covered with a large framework only containing very young, short, ramifications, in which only a few "germ-spheres", but a fair number of fully developed cercariæ are found. The hermaphrodite gland seems untouched, the albumen gland seems to be quite obliterated, the oviduct is rather well-developed but less folded than normally; the male part of the sperm-oviduct is strongly reduced, and the penis and vas deferens remarkably slight. — The spermatheca is present but very small. Both parts of the sexual organs are affected, the most conspicuous feature is the total loss of the albumen gland.

No. 3 (Plate IV, Figs. 1—2) is a very old snail, at all events three years old. It was found on $^8/_7$, at that time presenting two sacks, one in each of the antennæ. During the time from $^8/_7$ to $^{15}/_9$ the sacks pump uninterruptedly the whole day, but from $^{20}/_8$ only one very large sack is seen, the other is lying behind the antennæ and often pumping in a peculiar manner which I do not understand. From $^{16}/_9$ to $^{22}/_9$ they are often withdrawn and the snail sits cemented to the vessel without taking any food. When brought back to the leaf, the extremely thick antennæ are stretched out, and suddenly one of the sacks appears in the left antenna; suddenly this antenna is extremely distended. The next day the snail is again sitting half withdrawn in its shell. It seems very feeble; on $^2/_{10}$ it only reacts very slowly to the needle. The snail is now faintly narcotised and dissected. It shows two very large sacks, of these one is kneed. The sacks are seen pulsating below the skin behind the antennæ, and that in such a way that the knee fills up almost the whole space in front of the opening to the antennæ (Pl. IV, Figs. 1—2). It has become rigid in this position, and cannot be stretched out without breaking. The foremost part is pulsating. The other sack is peculiarly curved and extremely thick in its hindmost part. Of the sporocyst only very little is left; it is very old and its power of producing new sacks is unquestionably almost exhausted. — The generative organs of the snail are very greatly reduced. The hermaphrodite gland is but small; of the sperm-oviduct a small black portion is left; the rest is only a straight string and so also are the two separated parts, the oviduct and the vas deferens. There is no albumen gland. The penis is also much reduced; a small spermatheca is present. — The two sacks contain all the cercariæ of the sporocyst, about 500 altogether. If the snail had died a natural death, they would have become free during putrefaction.

No. 9 (Plate III, Figs. 3—5) is a very young snail; most probably not a year old, it was found on $^8/_7$ and at that time had one sack in each of the antennæ. On $^7/_8$ I amputated the right antenna; the sack did not come out but was always seen lying behind the sack of the left antenna. This had increased enormously in size by $^{20}/_8$. From $^{25}/_8$ to $^6/_{10}$ the snail never shows sacks; but several large sacks are seen pulsating behind the antennæ; it creeps about very slowly, but does not eat anything. On $^3/_{10}$ the snail is dying, and on $^6/_{10}$ in the morning it dies. Section is carried out while the sacks have still the power of motion. It shows that the body cavity of the snail consists almost entirely of *Leucochloridium*; it contains six large sacks all pigmented and all pulsating. The moment a small slit is made, all six sacks dart out. The sporocyst is very large; it lies on the outer side of the liver and sends a number of small threads into the body cavity. Of these threads five are relatively large white sacks, rather sharply set off from the thread; they contain cercariæ and numerous germ spheres. Of the genital organs only the hermaphrodite gland is fairly well developed, but all the rest of the organs are reduced to very thin strings; the albumen gland does not exist; there is not the slightest swelling of the sperm-oviduct; it is a simple string. The spermatheca is only represented by a string very slightly distended at the blind end. On comparing the figure of the *Leucochloridium* (Plate III, Fig. 4) with that of the shell, it seems almost incredible that the enormous parasite has had room in the snail Fig. 5, and that it has been able to live with it. It is rather peculiar that all these six sacks are pigmented. It would seem that the light shining through the skin of the snail is sufficient to produce the pigmentation of the sacks.

No. 12 (Plate V, Figs. 8—10) is also a young snail of middle size and most probably not more than one year old. It was found on $^{28}/_{7}$ and at that time showed two large sacks, one in each of the antennæ; during the time from $^{28}/_{7}$ to $^{26}/_{8}$, one or two sacks were always seen pulsating. On $^{26}/_{8}$ a very large pulsating sack is found lying on the leaf. Already on $^{8}/_{9}$ the snail again shows two large pulsating sacks. From $^{12}/_{9}$ to $^{17}/_{9}$ the snail is always entirely withdrawn in its shell; the foot only reacts very feebly to a needle. The snail was narcotised and killed in sublimate formaline on $^{25}/_{9}$ and then immediately dissected.

It showed two enormous fully developed sacks almost as long as the whole snail and extremely thick, two others almost fully developed, and some smaller ones. The sporocyst was situated in the liver and also in the hermaphrodite gland; of the albumen gland there was not the slightest trace, but the dark part of the sperm-oviduct showed some small windings; the rest of the organs were only thin strings; the spermatheca had almost become obliterated. When the large sacks were taken out of the body cavity, this was almost empty, containing only the alimentary canal and the liver, much reduced in size. It is rather peculiar that the penis sack is so greatly reduced and only present as a very thin string.

No. 15 (Plate V, Figs. 3—4) is another very young snail, most probably not one year old. It was found on $^{28}/_{7}$ and at that time showed two sacks, that on the left side being very small. From $^{16}/_{8}$ it shows only the large sack, and from $^{7}/_{9}$ to $^{6}/_{10}$ when the snail is dying, none. When taken for dissection, the snail shows one large sack and three smaller ones, but all pigmented and pulsating, besides two smaller ones and a rich net of ramifications in the upper part of the liver. Of the sexual organs only the hermaphrodite gland is not much affected, all the rest are only very thin strings; the penis is extremely thin. The parasite is an example of an extremely rapid development, most probably causing the death of the host even in natural conditions. In Fig. 4 is drawn the shell with the same power as Fig. 3. It will be understood what an enormous parasite the *Leucochloridium* really is.

No. 24 (Plate VI, Fig. 8) is an older snail, most probably two years old. It has been mentioned at p. 120. It was dissected without killing it. It showed one enormous sack and two smaller ones; the first showed no motion at all, the other two only slight motion; the sporocyst exhibited a great number of rather short club-shaped threads, some of them a little larger than the others. The hermaphrodite gland was present, but the sperm-oviduct as well as the male and female part of it were reduced to simple strings; no albumen gland was present. On the other hand, the penis had its normal size and appearance, and the spermatheca was also well developed. I think that these facts must be interpreted to mean that the snail has been infested rather late, most probably after the sexual organs have been functioning some time.

No. 28 (Plate IV, Figs. 3—4) is an old snail found on $^{12}/_{9}$. It shows two short thick antennæ but no sacks. During the time from $^{12}/_{9}$ to $^{30}/_{10}$ it never showed sacks; from $^{7}/_{10}$ to $^{30}/_{10}$ it was sitting cemented to the vessel, when it was taken for dissection. It exhibited two large sacks, one of them, evidently very old, was bent, dark brown, and strongly pigmented. Most probably it had formerly been larger. The sporocyst itself had only few other sacks, some of them were of a very peculiar, irregular form; it only contained cercariæ, no germ spheres; it was evidently very old and near the end of its power of reproduction. It was dissected out of the liver with all its branches and some of it drawn in Fig. 2., Plate II. In the central part, at the lower edge, are seen the two dark branches which have carried the two large sacks. It is of a rather yellow colour, not white like those in full vigour. The sexual organs showed a peculiarly high developmental stage. The hermaphrodite gland was well developed, as also the upper part of the black sperm-oviduct; the albumen gland was rather small, but the female part of the sperm-oviduct remarkably well developed, and with rather large windings. It contained balls of living spermatozoa. The spermatheca was almost normal, the penis sack somewhat reduced, especially in its upper part. It would seem as if the parasite here, in the lifetime of the snail, perhaps as an intermediate stage, was about to alter a hermaphrodite organism into a one-sexed one, and in this case into a male; we will return to this point later on.

No. 45 (Plate VI, Figs. 5—7) is a large snail, at all events two years old. It was found on $^{8}/_{7}$ and at that time showed only one medium-sized sack. On $^{16}/_{8}$ it showed two, these had grown up to two very large ones on $^{6}/_{9}$. From $^{16}/_{8}$ to $^{15}/_{9}$ one or two sacks were always pulsating; from $^{15}/_{9}$ to $^{22}/_{9}$ they were only rarely visible; the snail was half withdrawn and was unquestionably very weak. It was narcotised and dissected. It showed seven sacks, all of almost the same size; the sporocyst was large, filling up the greater part of the liver, but had no medium-sized sacks. It seemed as if the whole content of the snail consisted almost entirely of the *Leucochloridium.* The genital organs were extremely reduced. This will best be understood if fig. 5 (Plate V) is compared with a drawing of the normal sexual organs (Plate V, Figs. 1—2). — They are drawn with a high power in fig. 6, Plate V. The hermaphrodite gland is much reduced; the sperm-oviduct is only a thin string; there is almost no albumen gland, the oviduct shows no windings, only some irregular diverticula, and the vas deferens is but a very thin string. The penis is strongly reduced and the spermatheca almost obliterated.

No. 47 (Plate III, Figs. 8—10) is a medium-sized snail. It was found on $^{13}/_{8}$ and brought into the laboratory. Upon arrival here, it voluntarily threw off five large sacks which were all hanging out of the snail, all connected with the sporocyst by means of their threads. All were fully pigmented and all simultaneously pulsating. The aspect of the snail with these five pulsating sacks, which, taken together, almost took up as much space as the snail itself, was very peculiar. The snail was killed in warm sublimate formaline and then dissected. Taken out of the shell, it harboured, in addition to the five already mentioned, two other sacks, almost fully developed, and both strongly bent (Fig. 10). The sporocyst was very large, lying normally on the liver and giving off several long white club-shaped threads. The hermaphrodite gland was remarkably large, there was almost no albumen gland; the sperm-oviduct was rather well-developed with some well-defined windings, but the two separate parts of the sperm-oviduct were only two narrow strings, and so also was the penis; a spermatheca was strongly reduced. The genitalia of the snail are given with a higher power in Plate V, Fig. 7. In this case it seemed as if the body cavity almost only contained the parasite. Only the hermaphrodite gland was well developed.

No. 48 (Plate VI, Figs. 1—2) is a very large old snail found on $^{12}/_{9}$. It immediately showed one large and a smaller sack. It was very sluggish. It was narcotised, fully stretched out, and later on dissected; it had four free sacks, one of which was large, and several small ones only slightly pigmented. Furthermore on the outer side of the liver were found two rather large sacks strongly bent in and over each other, and very hyaline. The pigment was only faintly developed. The sacks contained a great number of agamodistomes (Plate VI, Fig. 2). As the sacks were rather narrow, not broader than the cercariæ, these were arranged regularly transversely to the long axes of the sacks and on a line. The curious thing was that the snail, in spite of the enormous development of the parasite, had rather well-developed sexual organs (Plate VI, Fig. 1). The hermaphrodite gland was almost of the normal size; there was a remnant of the albumen gland, and the sperm-oviduct showed a series of rather well-developed windings; only the two separate ducts and the penis were rather feebly developed but a spermatheca was present.

No. 5 (Plate VI, Fig. 3) is a little snail, at all events only one year old. It was taken on $^{13}/_{8}$ and then showed one large sack in the left antenna; the sack was almost always pulsating. On $^{7}/_{9}$ another, very large, sack was observed in the right antenna. During the time from $^{12}/_{9}$ to $^{17}/_{9}$ the large sacks were often withdrawn and often pulsating. From $^{17}/_{9}$ to $^{25}/_{9}$ the snail sat half withdrawn in its shell and took no food. On $^{25}/_{9}$ it was found dead and immediately taken for dissection. It contained two very large sacks, one of them bent and not capable of being straightened out without being broken. — The sporocyst was very large but only had these two large sacks. The sexual organs were only in part well preserved, this was especially the case with the sperm-oviduct; the rest were mainly thin strings; this applies especially to the penis. The spermatheca was but slight and there was no albumen gland.

No. 21 (Plate III, Fig. 2) is a rather large snail, most probably two years old. It was found on $^{13}/_{8}$ and on $^{16}/_{8}$ showed a large sack in the left antenna; on $^{7}/_{9}$ it had a smaller one in the right one; during the whole time from $^{16}/_{8}$ to $^{27}/_{9}$ it was always pulsating either with one or with two large sacks. On $^{27}/_{9}$ it was narcotised and immediately dissected. It shows one large sack; two smaller ones, all pigmented; the sporocyst is very large; it has reached the hermaphrodite gland. There is no albumen gland. The sperm-oviduct seems at the first glance to be normal, with many deep and conspicuous windings. A closer examination shows, however, that it is in reality in a peculiar stage of decomposition. It is gelatinous, contains no spermatozoa, and dissolves into a yellow or blackish-white matter as soon as it is touched.

The rest of the organs are merely strings, the penis is the best preserved part; there is a small spermatheca.

No. 22 (Plate IV, Fig. 5) is the snail mentioned on p. 99. It was kept under observation for more than eight months. When cementing itself for hibernation, it had two small sacks which increased steadily in size from $^{23}/_{3}$ to $^{20}/_{4}$. On $^{20}/_{4}$ the snail ceased to eat and died on $^{25}/_{4}$. When dissected (Plate IV, Fig. 5) it showed the two large sacks, curiously irregular, evidently very old; this at all events is the case with one of them, because it was observed already on $^{13}/_{8}$. But behind these two large sacks lies another of very irregular form with a peculiar knob on the foremost part, and vertical to its longitudinal axis; the form is somewhat like a bag pipe; it does not show the slightest trace of pigmentation, but in volume it is almost as large as one of the other two large sacks. The strength of the sporocyst itself is evidently almost exhausted; there are no young club-shaped sacks, and the whole framework is but slightly developed.

The liver is very small and the whole sexual system almost reduced to nothing; it shows quite the same stage of reduction as Fig. 5, Plate V; the hermaphrodite gland is present, but the albumen gland and the spermatheca have disappeared and the sperm-oviduct and the two separate canals as well as the penis sheath are all reduced to mere strings. — I tried to count the number of cercariæ in the whole sporocyst with its three sacks. It was not so very high, at the lowest 400, and not exceeding 500.

No. 50 (Plate VI, Fig. 4) is a very young snail, perhaps not one year old; it was found on $^{20}/_{7}$. During the time from $^{20}/_{7}$ to $^{15}/_{9}$ it almost always showed one single, steadily increasing very large sack, which, when fully distending the antenna, almost seemed as long as the snail itself. The last days of its life the snail was sluggish and ceased to eat. It was narcotised and dissected and then showed a single enormous sack lying above the alimentary canal and partly covering the liver; it took up more than half of the volume of the body-cavity. Only two other, small, sacks were found. The sexual organs were still rather well-developed, though certainly not able to function; the albumen gland was strongly reduced, and the windings of the sperm-oviduct not fully developed. The snail is a peculiar example of the fact that a sporocyst, when it is young, most probably begins with the development of a single sack which may reach an enormous size, and must be removed before there can be room for the development of new sacks. As soon as a bird has taken this large sack, there is plenty of room in the body-cavity and a whole number of sporocyst sacks may be developed, which again causes the total destruction of the sexual organs.

No. 51 is a very old snail, most probably more than two years old. It was found $^{20}/_{7}$ and at that time had very large, thick antennæ. During the period from $^{20}/_{7}$ to $^{5}/_{9}$, when it died, it never showed any sacks; it was always very sluggish; commonly it sat with the antennæ withdrawn and did not eat anything. On $^{5}/_{9}$ it died and was then taken for dissection. It showed highly interesting facts. It contained remnants of a single very large sack, very irregularly twisted; of the liver there was hardly the slightest trace, only a small portion in the uppermost winding round the hermaphrodite gland. But in the place of the liver there lay a large quantity of agamodistomes entirely free; of the sporocyst no trace could be observed. This was evidently the last stage in the development of the parasite, which caused the agamodistomes, when the snail was decomposed, to flow out on to the leaves. The snail almost exclusively contained agamodistomes. The hermaphrodite gland was present, but the rest of the sexual organs were merely strings.

No. 75 (Plate III, Fig. 1) is a very old snail; it was found on $^{12}/_{9}$ 26. The antennæ were very thick. It died on $^{15}/_{10}$ and never exhibited any sacks in the antennæ. During the whole time the snail was extremely sluggish and would never eat. When dissected, it showed no less than six sacks all pigmented, all almost of the same size, and all rather small. Most probably we have here an example of the fact that the snail has got rid of one or two very large sacks, and in the free space of the body-cavity six sacks have been simultaneously developed. Of the liver only very little was left; the hermaphrodite gland was small and the rest of the genital organs reduced to mere strings.

From the above observations it is possible to draw the following conclusions.

a. As mentioned above, the sporocyst only rarely sends its threads directly into the hermaphrodite gland, and I have never found them in the other parts of the sexual organs. These are not in direct contact with them, but nevertheless they are often very extensively destroyed. Apparently the snails behave in a very different manner in this respect. Snails may be found whose sexual organs are rather well developed and which nevertheless carry a large sporocyst; furthermore I have often found snails with hardly any sexual organs at all and with a very slightly developed sporocyst. Undoubtedly the age, state of nourishment, season and other factors, such as the disengagement of old sacks must be considered.

The albumen gland is the part which seems first of all to be affected; it is reduced in size, and may totally disappear.

Then the sperm-oviduct is affected; through a stage of decay in which it gets a jellied structure, it shrinks into thin strings.

The spermatheca wastes to a very inconspicuous appendix.

Penis is altered to an extremely thin string.

Finally the whole sexual apparatus is reduced to the hermaphrodite gland; and the sperm-oviduct, which is normally very thick and furnished with numerous windings, is reduced to a very thin thread.

b. The hermaphrodite gland continues the production of spermatozoa and, however thin the strings may be, spermatozoa seem always to be present. On the other hand, the production of eggs often seems to cease; they do not get down into the sperm-oviduct, and at all events get no material from the albumen gland.

With some right it may be maintained that many parasitised snails pass through a male stage or, in other words, that the parasite alters a hermaphroditic organism into a male. As a rule this stage does not last long, and most probably the animals never function as males.

In this, as in so many other cases, we have to do with a parasitic castration.

c. Several times I have found very old large snails with very deformed antennæ, though they never exhibited sacks. When they were dissected, it could be shown that the sporocyst was very old; no sacks were developed, or the snail contained one or two leathery, twisted, flabby sacks. In these cases the snails almost always showed well developed sexual organs. As far as I can see, we are here concerned with a case which is otherwise well known in parasitism, viz. that the castration, if the parasite succumbs, may cease, and normal conditions reappear. The more pronounced the parasitism is, the more must the snail draw upon its metabolic products for the nourishment of the parasite. Simultaneously the breaking down of the albumen gland goes on; this may most probably be regarded as an organ in which material is stored up for the brood; it may best be sacrificed and drawn into the metabolism for the benefit of the parasite. The demands of the parasite are enormous, and force the animal to consume great amounts of nourishment.

On the other hand, when the parasite perishes, the metabolism changes and the snail is able to work and to build up its sexual organs again.

Whether the snails will again be able to function is questionable, but it is beyond doubt that the hermaphrodite gland again begins to produce eggs as well as sperma; the sperm-oviduct again acquires its wrinckled appearance, and the albumen gland increases in size.

d. There is no doubt that the infestation with the parasite is extremely harmful to the snail. There is not the slightest trace of a static relation between parasite and host; the latter is forced to work extremely hard if it is to satisfy the demands of the parasite; the host must provide food for two and dispose of the waste products of two, the snail itself and its parasite. On the other hand, here, as so often, it seems as if the parasite is only rarely the direct cause of the death of the host, which would, indeed, be detrimental to the parasite itself. If only copious nourishment is given, the snail may live for months and often for years with the parasite. Snails which were unquestionably at least two years old, have been found with two large sacks in the latter part of June 1928; they have lived in the laboratory from June 1928 to the latter part of April 1929. Knowing that the development of the sporocyst to the stage when it is able to produce the large pulsating sacks takes at all events about three months (Heckert), we are justified in concluding that the snails must have become infested the preceding year (1927), and have hibernated twice with the parasite, i.e. about two years. That they have hibernated in 1929 is certain, and that they have hibernated twice is highly probable, since in 1928 three months before they were found, they were in the hibernating stage, and the majority of birds able to throw the eggs of the parasite had not arrived.

How enormous a parasite *Leucochloridium* really is in comparison with the snail will best be understood if we cast a glance at Plate V, figs. 3—4. Perhaps this will appear even more plainly from a study of Plate IV, figs. 7—8. The two sacks and the shell are drawn with the same power. The snail was kept alive for a month and then killed. It contained a large sporocyst, many small sacks, and the two large ones (Fig. 7); the rather well developed sexual organs are drawn in fig. 8. When the snail was killed and the two sacks were dissected out, I tried to put them into the shell again; it was, however, almost impossible to get room in the shell for the two sacks alone.

JOHNSTON (1920, p. 363) has observed that the mass of developmental stages of *Echinostoma revolutum* may be so heavy that in quantity it was about onethird the size of the viscera of the snail.

At my request Dr. BERG has been kind enough to determine the weight of the *Leucochloridium* in comparison with that of the snail. The weighing was carried out on the aperiodic weight of the laboratory. The animals were first weighed in the wet condition, later on the dry stuff of snail and *Leucochloridium* was determined.

The snail was taken out of the shell, and the sporocyst with all its ramifications and sacks dissected out of the shell. Snail and parasite were then laid on filtering paper till all fluids which could be sucked out had disappeared. They were then removed from the paper and put in a cup.

The result was as follows:—

In the wet condition:		Dry stuff of snail and *Leucochloridium*:	
Snail ÷ shell + cup	1.1538 gr.	Snail + Cup	6.8385 gr.
Cup	0.8830 -	Cup	6.7948 -
Snail	0.2708 gr.	Snail	0.0437 gr.
Leucochloridium cup	1.8231 gr.	Leucochloridium + Cup	1.7755 gr.
Cup	1.7675 -	Cup	1.7675 -
Leucochloridium	0.0556 gr.	Leucochloridium	0.0080 gr.

It will be seen that in both cases the weight of the *Leucochloridium* was about $^1/_5$ of the total weight. The weight of the shell was 0.0715 gr. I am quite sure that the weight of the *Leucochloridium* might constitute a much greater part of the total weight.

HURST (1927, p. 362), with regard to *Echinostoma revolutum*, arrives at the result that the highest percentage of parasites was that "in which they made up approximately one fifth of the total weight; furthermore (1927, p. 363) that in a healthy snail the soft parts are heavier in proportion to the weight of the shell.

As mentioned above, we are with regard to *Leucochloridium*, as far as I can see, concerned with a "castration parasitaire indirecte" best known through the investigations of GIARD and BONNIER (1887) (Les Epicarides). CAULLERY (1922, p. 255) quotes as another example the *Liriopsis* parasitising *Peltogaster*. In *Peltogaster* which carries *Liriopsis* the oocytes in the ovary are always degenerate; when *Liriopsis* is fullgrown, it ceases to take food, and when it is dropped off, a hole remains in the body of *Peltogaster*; through this hole *Liriopsis* has been fastened to it. The *Peltogaster* which have been infested with *Liriopsis* again begin to develop their sexual products. In other words, it is exactly as in *Leucochloridium*, the parasite uses for the building of its own body the material which the host should have used to develop its ovaries. When parasitation ceases, the metabolic processes change, and the host can once more begin to develop its sexual products.

The snails with which we are concerned are hermaphrodites. The parasite treats the hermaphrodite gland in such a way that the oocysts are first and most thoroughly destroyed. In the life history of host and parasite a moment may arrive when the hermaphrodite is more of a male than a hermaphrodite. As is well known, Smith (1910—11) has shown that male *Inachus* which have carried *Sacculina* are able to develop the sexual products again when parasitation has ceased; in this case, however, not male but female sexual products are produced. Simultaneously the secondary sexual characters, the broad tail and the legs which are to carry the eggs, assume the aspect of female organs. The same has been observed in *Paguridæ* carrying *Epicaridæ*.

As far as I know, the *Leucochloridium* is the first example we know of a parasite which, when living in a hermaphrodite, causes it to become unisexual, whilst the snail, when parasitation ceases, may again become a hermaphrodite. If it is really able to act as a hermaphrodite is questionable, but it seems fairly certain that the hermaphrodite gland and the sperm-oviduct acquire their normal aspect again. With the researches on intersexuality in mind, a more thorough investigation of these matters with regard to snail and *Leucochloridium* would seem of interest.

Chapter II.

Some theoretical Remarks.

Merely the slightest study of the life history of the Trematoda will give the observer an impression of the enormous power of adaptation possessed by the organism. It seems as if there is an ever active interplay between the trematode and its host, its morphological structure, habitat, and customs. Apart from a few mainly marine exceptions in the development of the Trematoda, only one thing seems fixed, the first host must almost always be a mollusc, commonly a snail. If this mollusc is lacustrine or marine the development may present great variations in detail, but broadly speaking the normal scheme of development of all these Trematoda is as follows. From the egg thrown off in the water with the excrements is developed a miracidium, which, going in search of a mollusc, pierces its skin, whereupon it is there developed into a sporocyst. This sporocyst produces either daughter sporocysts or rediæ, daughter rediæ or cercariæ; sooner or later the cercariæ will normally leave the first host, live in the free state for a short time whereupon they encyst either in a secondary intermediate host, or upon the vegetation. Sooner or later they will reach the final host, where they mature, whereupon the eggs are again given back to the water with the excrements. The variations from the normal scheme are mainly adaptations in accordance with the structure and habits of the final host. We shall return to this point in the second part of this work.

A few Trematoda accomplish their development in molluscs which are terrestrial; of the development of all these Trematoda our knowledge is extremely restricted.

The more terrestrial the snail is in its habits, the more the trematode must alter its development and habits; very peculiar life histories are the result. However different their development is, a feature common to most of these aberrant forms is the loss of a free-living cercaria stage. The slightest adaptations occur in those cases where the land snail belongs directly to the diet of the final host. This is the case with the two living in *Erinaceus europæum*, viz. *D. leptostomum* and *D. spinulosum*, whose parthenogenetic generations are passed in species of the genus *Helix*, *Succinea* and *Arion*. The miracidium is not liberated from the egg till it arrives in the alimentary canal of the snail. From there it wanders into the liver, and is transformed into a ramified sporocyst in which cercariæ are developed. Later on these wander into the kidneys and are there developed into an agamodistome stage (*Cercariæum*). As such they remain till the snail is eaten by the hedgehog. Here the adult stage is reached, whereupon the eggs, passed out with the excrements, again proceed on their way to the intestine of a snail. The cercariæ are partly furnished with a short tail, partly they have no tail at all (Hofmann 1899, p. 176).

Highly remarkable conditions were found by Moulinié (1856, pp. 187—191). In *Limax rufa* and *L. cinerea* are found cercariæ with a very reduced tail, which is used as a sucker during the creeping motion. They develop into sporocysts which, according to Moulinié, in contrast to all other sporocysts force their way through the skin and are found as white dots partly upon the skin of the snails, partly in the slime from the slugs. The snail is said to deposit about 50—60 per day. The dots contain the cercariæ with an extremely short tail; deposited on plants they are said to live for several days. Sections show that the snail harbours in its organs numerous sporocysts of quite the same appearance as those which were found outside the body of the animal; notably they are common in the liver. Moulinié supposes that the sporocysts are devoured directly by other slugs, and that there is no other host at all. In this case the sporocysts are therefore supposed to play a similar role as a distributing factor as the cercariæ in the life history of other Trematoda. These observations, now about 80 years old, have, as far as I know, never been corroborated later on, and renewed investigations are greatly needed.

In those cases where there is no connection at all between the primary and the final host, i.e. where the primary host is not food material for the final one, it is the trematode which must bring about such a connection, and this is just what the *Leucochloridium* does by means of its constantly pulsating and coloured sacks.

In this connection it may be added that even in those cases where the final terrestrial host is not voracious but lives on vegetable matter, the development of *Collyricum faba* seems to show that the normal scheme of development of the Trematoda can be altered so much that in that case too, an adaptation to these highly aberrant life conditions has been possible (JEGEN 1917, p. 460; TYZZER 1918, p. 267).

With regard to the *Leucochloridium* it is beyond doubt that it is to the sporocyst that the problem is committed of attracting the attention of the bird to such animals as do not always belong to their normal diet. For it must be remembered that many of the small songbirds which are to take the sacks of the *Leucochloridium* are never snail-eaters and are quite unable to swallow a *Succinea*. As this problem, as far as we know, has not been solved by any other sporocyst, it is easily understandable that just this sporocyst may differ greatly both structurally and biologically from all others.

How much it differs will be best understood if we cast a glance at the sporocyst as it is known in other Trematoda.

In the life of the trematode the sporocyst in the first place plays the following role. Starting from a single miracidium it so to speak overflows all organs of the snail by means of its propagation, and creates an enormous number of specimens which, by fresh acts of propagation, again augment these numbers, often to such a degree that the snail, shortly before its death, seems almost changed into one enormous living mass of parasites, and the water is coloured milky when the offspring from this same single miracidium is given off.

1. The propagation of the sporocyst is of a twofold kind, partly a division combined with the detachment of buds, partly parthenogenetic propagation (mother sporocysts, rediæ or cercariæ). The first-named form is maintained by many older authors (FILIPPI 1854, p. 331, PAGENSTECKER 1857) and also by many more recent authors (THOMAS 1883, p. 108; BIEHRINGER (1884, p. 108); HOFMANN 1899, p. 191; REUSS (1903, p. 469), FUHRMANN 1928, p. 80, BRAUN (1893, p. 806). Only SINITZIN (1909, p. 669) maintains that all reports of asexual propagation in the sporocyst are grounded upon insufficient observations. I do not think that this supposition is correct. I shall return to the question in the second part of this work.

The sporocyst of *Leucochloridium* has no propagation by means of division. From a miracidium there is never developed more than one single sporocyst; this, however, is of an enormous size. From the spot where the miracidium has fastened itself, the sporocyst grows, forms its long threads and club-shaped bodies which slowly expand over the whole surface of the liver. A *Leucochloridium* sporocyst may grow one or two years old, but during all that time it is the very same sporocyst, developed from the single miracidium which long ago made its way to the anchoring place which it has never left since.

2. Another difference is that the sporocyst in contradistinction to almost all other sporocysts is ramified. Ramified sporocysts are found in *Harmostonum leptostomum* from *Helix arbustorum*, where the sporocyst occurs as "netzförmig verzweigte"

organisms, which form "wahre Rasen" (HOFMANN 1899, p. 186); they have also been found in other landsnails by ERCOLANI (BRAUN 1893, p. 806); in *Limnæa stagnalis* (LEUCKART) developing in *cercaria ornata*. Also in the development of *Bucephalus polymorphus* do we find strongly ramified sporocysts (figured and described by LACAZE DUTHIER 1854, p. 294; TENNENT 1906, p. 635 and by ZIEGLER 1883, p. 537). Recently in *Panopistus magnus* from *Gastrodonta ligera* (SINITZIN 1931 p. 799).

From sporocysts of this form there is an easy transition to sporocysts whose threads cannot be disentangled, and whose extremely fine threads are interwoven to form white spots lying on or in the infected organ of the mollusc. Sporocysts of this nature always, as far as is known, give rise to furcoid cercariæ. It may be questionable if we are not here originally concerned with ramified sporocysts.

Even if ramified sporocysts are known from other Trematoda that of *Leucochloridium* deviates in its power of producing the pulsating, irregular, pigmented and coloured sacks, which force their way into the antennæ, into which the cercariæ wander, and where they are deposited. In this respect *Leucochloridium* is unique among all Trematoda. With regard to the pigmentation of the sporocysts in other Trematoda, and the role which the antennæ of the snails play as organs through which the parasites enter or leave the snail, either as miracidia or as cercariæ, I refer the reader to the second part of this work.

3. In most of the other Trematoda we see the sporocyst develop either daughter sporocysts, rediæ, daughter rediæ or cercariæ which leave the snail. In *Leucochloridium* the sporocyst only develops tailless cercariæ, which remain in the sporocyst and sooner or later pass into a stage which, from a biological point of view, is identical with a cyst.

With regard to the peculiar origin and structure of the envelope of the agamodistomes in *Leucochloridium* this seems at first to be an almost unique feature in the Trematoda. When during the last few years I had an opportunity of studying many *Tetracotyle* stages in *Limnæa stagnalis* and became acquainted with the literature of FAUST (1918a, p. 69), SCHEURING and EVERBUSCH (1926, p. 41); HUGHES, LA RUE and others (see list of lit.), I was struck by the great similarity between the envelope of the agamodistomes of *Leucochloridium* and the envelope of *Tetracotyle*. Later on when, in 1930, I became acquainted with the paper of SZIDAT (1929, p. 685) I saw that he had quite the same view. The two above-named structural peculiarities, ramified sporocysts and the conformity in the structure of the envelopes in *Tetracotyle* and the agamodistome stage in *Leucochloridium*, are just those characters which SZIDAT (1929, p. 685) among others has used to establish a closer relationship between the families *Harmostomidæ* and *Holostomidæ*.

4. Another great peculiarity in the sporocyst is the relatively extremely small number of cercariæ it is able to produce. Most probably it may be computed at only a few thousand. If we remember that a single *Limnæa stagnalis* or *Planorbis corneus* day after day is able to colour the water in our vessels or the small spaces among waterplants milky with xiphidioid-cercariæ and cloudy with Furcocercariæ, and that

Fuhrmann (1928, p. 90) in the course of four successive days has counted the following numbers of Furcocercariæ thrown out by a single snail (8000—5400—13300, and 15900), numbers which I can confirm and to which I shall return, it will be understood that the progeny of the *Leucochloridium* sporocyst is in reality very limited in number. Hence, as far as I can see, it is not correct when Bittner and Sprehn (1928, p. 107) maintain that the sporocyst of *Leucochloridium* "im Innern ungezählte Keimballen enthält".

5. Another peculiarity with regard to the *Leucochloridium* sporocyst is that the cercariæ never come out of the sporocyst, but remain here until the final host liberates them. The cercaria stage has entirely lost its significance as a distributing factor. (With regard to the cercariæa stages developed in watersnails (*C. paludina impuræ*) see the second part of this paper).

An approach to this highly interesting peculiarity is, however, found in those cases where the cercariæ have a well developed tail but nevertheless the whole development takes place in the snail. In these cases, too, the power of distribution of the cercariæ is often much restricted. In numerous cases the cercariæ, the very moment they have been expelled from one snail, plunge into another lying near the first; and very often, if no other snails are present, they fasten themselves on the snail which they have just left. The tail is thrown off, whereupon they pierce a hole in the skin. Cort (1915, p. 37) shows that echinostome cercariæ (*cercaria trivolvis*) may use the same animal (*Planorbis trivolvis*) both as their primary and their secondary host (see also Faust 1917b, p. 35; Moulinié 1856, p. 137; Fuhrmann 1928, p. 88).

The last stage which, from a biological point of view, is very nearly related to what we find in *Leucochloridium*, is represented by those cases where the cercariæ never leave the mother organism in which they are developed. Johnston e.g. (1920, p. 362) has found in *Echinostoma revolutum* 58 rediæ with cysts, and very often rediæ which contain both rediæ and cysts. He maintains that, in the *Echinostomata*, encystment in the same host in which sporocysts and rediæ have been developed will be a common family character. Loos (1894, p. 48) has found as many as 40 cysts in the same sporocyst, and Lebour (1907, p. 102) has found in *Cardium edule* a sporocyst which contained cercariæ as well as cysts; she furthermore observed that the cercariæ in the sporocyst throw off their tail and that the tail moved for a time after being thrown off. With regard to my own investigations and experiments on this subject I refer the reader to the second part of this work.

In all these cases the significance of the cercaria as a distributing factor in the life of the parasite is lost, nevertheless the stage is retained. Here as so often the species is altered biologically before being transformed morphologically. From a developmental and morphological point of view there may very well be differences between the encysted stages in the sporocysts of watersnails and the agamodistomes in the sporocysts of *Leucochloridium* but from a biological point of view the significance is the same.

Even if we can find related traits in the structure and behaviour of other sporocysts, there is no doubt that the *Leucochloridium* sporocyst in its structure and development deviates more from the normal than any other sporocyst hitherto known.

For years I have worked with *Leucochloridium* from a conviction that our knowledge of the development of *L. macrostomum* is in reality very sporadic, and that the whole development in *Succinea*, from being originally an abnormal, almost a pathological, phenomenon, has at last become normal and useful for the species; the original normal development may perhaps still be going on, but of its details we know nothing. For years I have tried to prove this theory; I confess, without the slightest result. The working theory may be wrong; but I am not sure that it is so. My failure may be due to the fact that the theory cannot perhaps be proved in our latitudes, the proof of its correctness belonging to more southern countries. It is especially with this supposition in mind and hoping that the theory will be tried in other latitudes, that I take the liberty of setting forth the considerations on which the working theory has been based, and the way I have gone to support it.

ZELLER's and HECKERT's investigations show that the agamodistomes in the sacks of *Leucochloridium* reach maturity when transferred into the alimentary canal of Passeres.

If the developmental possibilities of *L. macrostomum* were exhausted with this, it must be admitted that with regard to the development of *L. macrostomum* nature has solved problems which might *a priori* be regarded as insoluble.

The problem which the sporocyst so to speak had to solve and really has solved, was to remodel the antenna of a snail, an organism in which the bird was not normally interested, into an organ which, in the eyes of the bird, should look like an insect larva and in this way alter it into desirable food material. The antenna now causes a reflex action on the part of the bird, owing to which the snail now, in spite of earlier experience, attracts the attention of the bird, whereupon it is also, itself, through the sack as a transitional stage, transformed into desirable food material. For it must be remembered that even if it is only the sack which attracts the bird, it cannot be unaware that this sack is in some way connected with the impression of a snail. Furthermore it must be kept in mind that this process, which is highly remarkable from a morphological and biological as well as from a physiological point of view, is a result of mimetic phenomena, and that in a group of animals where mimetic phenomena, as far as we know, have never been observed before.

Finally these mimetic phenomena occur in an organism whose place is in the interior of the snail, and whose organisation is of the greatest simplicity. As mentioned above, as far as we know, it has no nervous system and no sensitive organs of any kind. Nevertheless it reacts to stimuli from without (variations in light and temperature), and localises this power in special parts of the body which are capable of locomotion in a quite special way.

If we further remember that no one has hitherto, in natural conditions, seen a bird split the antenna of the snail and fly away with the sack to the nestlings, it cannot be denied that there is still room for some doubt. Especially with this latter point in mind, it may be allowable to suppose that our knowledge of the life history of the trematode is not fully exhausted with the feeding experiments of ZELLER and HECKERT. In my opinion this will be even more obvious if we take some other points into consideration.

Our knowledge of the tribe *Leucochloridea*, its species and their systematical relations, has always been extremely restricted. The new treatment of WITENBERG is, as far as I can see, by no means able to dispose of heterodox opinions.

WITENBERG (1926, p. 227), in his treatment of the family *Harmostomidæ*, maintains that there exist at all events four species of the genus *Leucochloridium* (*Urogonimus*) one of which is undetermined. The other three are *L. macrostomum* (Rud.), *L. insigne* (Loos) and *L. turanicum* (Soloviev). Other species described as *L. cercatus* (Monticelli), *L. assamense* (Sewel) are either insufficiently described or larva stages. It was RUDOLPHI (1802, p. 26) who created the species *Distomum macrostomum* found in *Motacilla*. When in 1819 (p. 94) he found new specimens in *Fulica atra*, he referred these specimens to a new species *D. holostomum*. According to the description it seems that the only difference is a difference in size: *D. macrostomum* is smaller than *D. holostomum*. BRAUN (1901, p. 500) who has studied the type specimens, arrived at the result that the two species were identical and, as far as I know, all later authors who have made *Leucochloridium* the subject of a more thorough study, have arrived at the same result (HECKERT, MÖNNIG and MAGATH).

If this view is correct, this would in other words mean either that we must expect to find the *Leucochloridium* sporocyst in real water snails, or that the water-birds get their parasite from feeding on *Succinea*.

WITENBERG, however, arrives at the result that the two species *D. macrostomum* and *D. holostomum* differ from each other. ("Indes gehören zweifellos die Exemplare von der Bachstelze und vom Wasserhuhn zu verschiedenen Arten" p. 233.) As far as I can see, he gives no other reason for this supposition than that they are found in birds belonging to different orders, perhaps also because we know a series of sporocysts, of which those with green and brown sacks are parasites in *Succinea putris*, whereas those with yellow and golden-red ones are parasites in *Succinea retusa* and water snails (species belonging to the genera *Vivipara*, *Planorbis* and *Limnæa*). WITENBERG (1926, p. 228) further maintains that all those older species are insufficiently described; on this point WITENBERG is certainly quite right. How insufficient our knowledge of the species actually is, will best be understood from the fact that the species with which HECKERT has worked, according to WITENBERG (1926, p. 232), is neither *L. macrostomum* nor *L. holostomum* "sondern irgend eine andere, wahrscheinlich *L. insigne*" (Loos).

L. insigne is found in *Actitis hypoleucos*, *Totanus ochropus* and *T. glareola*. This means, in other words, that, since HECKERT got his specimens from songbirds[1], this

[1] "Als die eigentlichen und natürlichen Träger des geschlechtsreifen *Distomum macrostomum* möchte ich aber meinen Erfahrungen zufolge die Sylvien in Anspruch nehmen". 1889, p. 26.

species should be able to live in Passeres as well as in waterbirds. As far as I can see, WITENBERG himself has given a proof of the incorrectness of his supposition that "jede aus den 3 von mir bezeichneten Arten einer spezifischen Gruppe der Wirte entspricht".

If BRAUN, HECKERT, MÖNNIG are right in their contention that *L. macrostomum* and *holostomum* is the same species, it is found in a long series of insect-eating *Passeres* as well as in many waterbirds e.g. *Rallus aquaticus, Porzana porzana, Gallinula chloropus,* birds which find their food in localities where *Succinea* may be found, which are really snail-eaters, but mainly live of typical water snails and swallow the snails whole. They are therefore by no means specially attracted by pumping sacks. — But more than that, the ripe stage is also found in a long series of typical seed-eaters such as *Passer montanus, Fringilla coelebs. Pyrrhula pyrrhula, Carduelis linaria.*

How is it possible to understand that these birds, which are neither snail nor larvæ feeders, should split the antennæ of *Succinea* and so become infected. As hosts are also stated *Garrulus glandarius, Corvus corone,* further *Picoides tridactylus(?)* and *Dryobates martius*(?). Even if the two first-named might get the parasite when eating nestlings in the nests of *Sylvias,* how can we explain that the two last-named get it?

Recent investigations furthermore strengthen the view that what we know with regard to the development of the different *Leucochloridium* species is extremely little.

MAGATH (1920, p. 110) found a new species of sporocysts in a Succinea (*S. retusa*) as well as in *Planorbis trivolvis*; LUTZ (1921 a, *L.* sp.) in *Hapalonyx*; FAUST (1924, p. 258) another sporocyst *L. millsii* in *Limnæa plicatula.* This shows that the development of the *Leucochloridium* species may take place in typical water snails. When *Leucochloridium* species are found in waders, which mainly live on water snails, and these cannot be distinguished from those in *Sylvias,* it may be permissible to suppose as a working theory that the development of the same species may take place in typical water snails as well as in *Succinea,* furthermore that the development in the first-named may take another course than hitherto known. The latter supposition is somewhat strengthened by an observation by SEWELL, which, however, stands greatly in need of verification. SEWELL (1922, p. 171) maintains that he has found young specimens of a species of *Leucochloridium,* which were "discovered in gelatinous yellow cysts in the thick edge of the mantle in specimens of *Lecythoconcha lecythis* and *Vivipara oxytropis* obtained by Dr. ANNANDALE in the Laktak Lake, Manipur. The cysts measured $1^1/_2$—2 mm. in length and about 1 mm. in breadth, and each communicated with the external surface of the mantle, that is, the surface in apposition with the shell, through a small pore. They contained immature *Leucochloridium,* measured 2—3 mm. in length and the hinder part of the body was of an orange-red colour". The trematode is described and figured on Pl. XVII, Fig. 3. SEWELL (p. 172) maintains that the structure of these forms agrees very closely with the description of *L. macrostomum* (Rud) given by HECKERT (1889). In accordance with this SEWELL quite correctly comes to the result" that the development of the *Leucochloridia* is not always the direct simple process that occurs in *L. para-*

doxum. In the present stage it seems certain that the sporocyst stage is followed by a free-living period, in which the cercariæ leave the original mollusc host, and migrate into and encyst in an intermediate mollusc host".

As far as I can see, our knowledge of the systematics and development of the group *Leucochloridea* is so restricted that it may be supposed that the last word with regard to the development of *L. macrostomum* has not yet been said. Furthermore, as stated above, it seems reasonable to see an abnormality in the hitherto known development of the species, which has been useful to the species in some of its areas of distribution, whereas the normal development, following the common scheme of development of Trematoda, in other of its areas is still going on. In my opinion this supposition is further strengthened if we take two other points into consideration.

1. In the history of helminthology two old theories of development have been set forth; both were very soon stigmatised as heretical; nevertheless it seems very difficult to do away with them. Again and again they turn up, each time in a new dress. The one is the theory of Ercolani (1881, p. 237) that the same trematode larva could, during accommodation in different hosts, develop into what we should be apt to regard as different species. The other is that of Filippi (1854, p. 275) that "un bon nombre de Trematodes aient cessé d'exister à l'état parfait ou ne se montrent dans cet état que rarement de temps en temps en des circonstances presque exceptionelles et que leur espèce ne se maintienne qu'à l'état imparfait".

The theory set forth by Ercolani is of course too massive in form. On the other hand it cannot be denied that the views of Loos (1899, p. 521) are related to those of Ercolani. Loos maintains that though flukes found in birds and mammals may be morphologically identical, they may be regarded as physiological varieties or species. The different habitat and different metabolic processes in birds and mammals would produce the differentiation. Fuhrmann (1928, p. 95) calls attention to the fact that in such different forms as birds and cats we have found species (*Opistorchis geminus* and *Opistorchis sinensis*) which it is impossible to distinguish from each other. In that case we are obliged according to Fuhrmann to suppose that we are here concerned with species which are anatomically identical but differ physiologically. We find related ideas set forth by Leuckart (1889, p. 171), who maintains "das nämlich durch Anpassung an fremde oder falsche Wirte neue Arten entstanden sein können". Leuckart thinks, that the parasites offer an extremely interesting field for investigation in this respect. It is a well-known fact that wherever we meet physiological races, we regard this as the beginning of a species-making process and that a closer examination has in fact more than once revealed small morphological differences between the races lasting as long as the races live under the same conditions of life.

I cannot see better than that these theories, set forth by Leuckart, Loos and Fuhrmann, are in reality only another, more modern, expression of Ercolani's old theory, or at all events nearly related to it. It is with these theories in mind that I consider it allowable to suppose that *L. macrostomum* may develop in other snails than *Succinea*, and that the development here may take another course than that known to us. It may be added that the opinion of Loos is not endorsed by Faust and Nishigori (1926, p. 121).

Even if the theory of Filippi cannot be maintained in its full extent it has at all events an element of correctness. For numerous species there may exist areas where the species may only or mainly occur in the parthenogenetic generations. In these areas the first and the intermediate host may again and again be re-infected, whereas the infection of the final host is very problematic; furthermore, in very many cases the developmental stages may find their way into or be taken up by hosts for which they are by no means destined. In many cases the result will be death, but in many others life is possible, and the new habitat gives rise to physiological and morphological races.

The more bound to the soil the first host is, the more sharply delimited it is from a systematical standpoint, the more the migratory instinct is developed in the final hosts, and to the more deviating systematical unities they may belong, the more we may expect cases in which the development of the parasite may be begun but not completed. Furthermore we may expect that metamorphoses may begin and may be completed but give rise to new physiological forms, perhaps morphologically deviating from the normal forms, especially with regard to size (dwarf forms, giant forms, variations in the strength of the organs of attachment etc.).

If we wish to understand the development of all those Trematoda which live as ripe stages in migrating birds, there is one factor, bird migration, which must always be taken into consideration. Only few have paid sufficient attention hereto; in the first place may be mentioned some American authors (Ward 1909, p. 1, and Johnston 1920, p. 369); further Sewell (1922, p. 12) with regard to India. Whereas in Europe (especially owing to the investigations of Zschokke (1902, p. 118), we are well aware of the relation between fish parasites and migration phenomena, we have not, as far as I know, studied the influence of migration upon the life of bird parasites. Only Loos has some remarks on this subject (1899, p. 522).

For 12 years Ward (1909, p. 5), aided by students and friends, made systematic collections of parasites from the migrants belonging to vast swarms of wild ducks of numerous species, which breed, some within the northern limits of the States, but mostly much farther north. Ward has made the very important observation that the parasites found in the birds going south are radically different from those they harbour on their way north some four or five months later; only a certain small percentage of the parasitic fauna of the two seasons is identical. Whether this element is acquired in both regions, or whether it is characteristic of one only and persists beyond the period of stay, is left undecided. One factor tends to confuse the results. Many of the birds which travel south in the autumn are young, having been hatched in that summer's brood; of course they are only infected by the parasitic fauna of the north. "But they are also in large part the parasites of immature age, and do not recur in the full-grown birds, even though the latter have passed the summer in the same environment". As far as I know, this extremely interesting account has not been followed up by a more elaborate investigation.

To accomplish a similar investigation of the songbirds in this country would most probably be an impossibility. All our songbirds are rigidly protected the whole year round, and their capture in nets or in any other way in which birds could be got in great numbers would not be allowed. Only during the passage from the light-houses could material perhaps be acquired, but in this case difficulties of another kind would arise. As is well known, *Succinea putris* is rather local in its distribution; the migrating songbirds use numerous localities as resting places during migration, in which *Succinea* are never to be found; enormous numbers of eggs may never reach their destination. Hitherto *Succinea putris* has not been found farther south than the northern coasts of the Mediterranean. As enormous numbers of ripe stages of the trematode may cross the Mediterranean in the cloaca of migrating birds, it would be of the greatest interest if it could be elucidated whether the African species of *Succinea* harbour *Leucochloridia*. Professor Steenberg has kindly told me that Africa harbours many and large species of the genus *Succinea*. From Marocco is recorded 1 species, from Algiers, from Northeast Africa 16, from Congo 6, from the Cameroons 1, from Niger and Lake Chad 2, from German East Africa 2, from Portuguese East Africa 3, and from South Africa 16.

If the life history of *Leucochloridium* were fully elucidated with the investigations of Zeller and Heckert, its course of life would be so sharply delimited, that it would seem almost unintelligible how the species could keep its place in nature. This is especially obvious if we remember the relatively very small numbers of cercariæ which are produced by the sporocyst, the enormous amount of sacks which never reach their destination, and that the final hosts are mainly or partly migrating birds.

With the above named ideas in mind I have examined many hundreds of *Planorbis* gathered in many localities, especially the lakes of Sorø and Esrom where *Fulica atra* are present in great numbers, (in Esrom Lake by thousands), and where *Gallinula chloropus* is common (in Sorø Lake). Nevertheless I have never had the good luck to find the parasite in these snails.

On the same *Petasites* leaves upon which I found my *Succinea* infected with parasites I always found *H. nemoralis, hortensis* and *arbustorum* in great numbers. But more than that: On the leaves of *Petasites* where the birds had dropped their excrements which contained eggs of Trematoda I very often found simultaneously and upon the same mass of excrements a *Succinea* as well as two or three *Helices* sucking. We are bound to suppose that the result for *Succinea* as an excrement-eater is that it gets its ramified *Leucochloridium* sporocysts in this way. The conjecture that *Helix* could also be infested was so much the more allowable, since the Helices also harbour ramified sporocysts with tailless cercariæ which develop in *Erinaceus* *europœus* to *Harmostomum leptostomum* (Hofmann and others) and belong to the same family to which *Leucochloridium* belongs. With these facts in mind I have taken 50 *Helix nemoralis* and *arbustorum* from the same *Petasites* leaves from which the infested *Succinea* were gathered and from the same excrement masses upon which the *Succinea* were sucking and kept them for months, but nevertheless not a single infested *Helix* was found.

Since very old snails, which had not shown sacks for months, but whose antennæ were deformed when dissected, showed cercariæa lying free in the liver, I supposed that the cercariæa could perhaps grow ripe in the snail and the bird be eliminated from the life history of the parasite. From recent years we have examples of trematodes, whose whole development is really passed in a single host (*Lecithodendrium chilostomum* in *Phryganea*; *Pleurogenes medians* in *Gammarus* and perhaps *Collyrichum faba* and Trematoda from slugs). With this thought in mind I have dissected about 50 infested *Succinea*, but always without result.

It must be frankly admitted that my above-named working theory, which has occupied me for more than two years, has by no means been verified. Nevertheless I feel convinced that it contains some grains of truth, and that the failure on my part is due to the fact that only investigations in other, more southerly, latitudes can prove its correctness.

Postscript.

After my paper was almost printed two papers by Halík and Sinitsin have appeared. The first paper deals especially with the pulsation of the sacks. There is only a single passage on which I take the liberty of offering some remarks. Halík writes (p. 462) "Diese Interpretation (of Siebold) ist deshalb interessant, weil wir hier das seltene Beispiel im Tierreich haben, dass ein Tier ein anderes durch Färbung und Bewegung nachahmt, nicht um geschützt sondern um gefressen zu werden, da nur auf diese Weise die *Leucochloridium*-Schläuche den nächsten Entwicklungsstadien, den Zerkarien, einen neuen Wirt und somit das Fortkommen einer neuen Generation sichern."

This remark is not new however. Zeller (1874, p. 577) has already put forward quite the same interpretation. He writes: "Wo wir sonst von "Maskierung" oder Nachahmung hören, soll diese immer zum Schutz und zur Erhaltung des betreffenden Tieres oder doch irgendwie zu seinem Nutzen dienen. Für unser *Leucochloridium* wird die Änlichkeit mit einer Insectenlarve nur zum Verderben. Denn was anderes wird durch dieselbe erreicht, als dass die Aufmerksamkeit eines Insecten fressenden Vogels erregt und dieser veranlasst wird, das *Leucochloridium* aus der Schnecke herauszufressen . . . Eine solche Absicht aber für seine Brut die eigene Existens zu opfern wird gewiss Niemand unserem *Leucochloridium* zutrauen wollen." He further says: "Unser Fall ist recht geeignet einen Beweis gegen die Annahme eines solchen Vermögens und die Anschauung, als ob die Thiere bei ihrer Maskierung eigentlich mit Bewusstsein handelten, zu liefern."

ZELLER's view was well known to me; nevertheless I have not mentioned it, because in my opinion it is not right. Now that I find the same view advanced in a recent paper, I take the liberty of calling attention to the following fact. Whatever supposition we generally may have with regard to mimetic processes, and more especially as to those which should have produced the resemblance of the *Leucochloridium* sack to an insect larva, one thing is beyond all doubt. The sack itself is not an organism, it is only part of an organism, and this organism persists for years after the liberation of the sack. ZELLER is not right when he says that "die Ähnlichkeit mit einer Insectenlarve nur zum Verderben für unser *Leucochloridium* wird", nor is HALÍK right when he says that *Leucochloridium* is an example of the peculiar fact "dass ein Tier ein anderes durch Färbung und Bewegung nachahmt nicht um geschützt sondern um gefressen zu werden." The liberation of the sack is an unquestionable advantage to the sporocyst, and the whole process is viewed by ZELLER and HALÍK from a decidedly wrong angle.

In many respects the liberated pulsating sacks are almost without parallel in the animal kingdom. From a biological point of view, as far as I can see, the *Leucochloridium* sporocyst can best be compared with those organisms which develop special parts of their body in which sexual products are deposited and which, provided with the power of locomotion, are loosened from the mother organism and are for a short time able to live an active life. The detached arm of the *Argonauta*-male, the loosened buds of the chains of some of the pelagic *Syllidæ* and other *Polychæta*, the pulsating sacks of *Leucochloridium* are all parts, detached from the mother organism and all play a role in the propagation of the species. At a first glance the comparison seems farfetched, but from a biological point of view a closer inspection will show that it is right.

To the interesting paper of SINITSIN I shall return later on.

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EXPLANATION OF PLATES

All plates reduced one third.

All figures are drawn with a Zeis microscope or with Zeis lupes and with a camera. Where the power or lenses are not indicated the power is 3—4.

Plate I.

Fig. 1. A *Leucochloridium* sporocyst with brown sacks . . . . a*. Sucherocular

\- 2. A *Leucochloridium* sporocyst with green sacks . . . . a*. Sucherocular

The size and form of the pigment bands are subject to very great variation, and the differences in the arrangement of the bands in the brown and the green sacks are not always so large as the figures show. The apex of the brown sacks is always brown; that of the green, as far as hitherto known, always red.

\- 3.} - 4.} Show two sacks from very old sporocysts; all pigmented sacks are thrown off; the production of germ spheres is stopped, the sacks are but small, very irregular in form, and contain only a very few agamodistomes; these are all opaque with very thick walls. In the strings, which are dark brown and without lumen, is found a single agamodistom which has not been able to force its way to the sack. It has blocked up the passage for other agamodistomes and is itself quite opaque . . a*. Oc. 4

\- 5. Section through a sack showing the arrangement of the agamodistomes . . . . a*. Oc. 4

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Plate II.

Fig. 1. A very, young sporocyst found in a young snail which had never shown sacks in the antennæ and which had lived for three months in the terrarium .... Obj. 16. Oc. 4

- 2. A very old sporocyst. At the lower edge is shown two dark branches which have carried large brown sacks. The other sacks are all small, very irregular in form, and carry branches of the second order. The production of germspheres has ceased, and fully developed agamodistomes are not present .... a*. Oc. 4

- 3. a.—e. The same sack drawn from a living specimen. The drawings show the great form variation, most conspicuous at the apex, f. is the same sack drawn immediately after it had been killed in formaline.

- 4. Transverse section of the sack. To show that the agamodistomes are lying so closely packed that the envelope gets pentagonal or hepagonal......... Obj. 16. Sucherocular

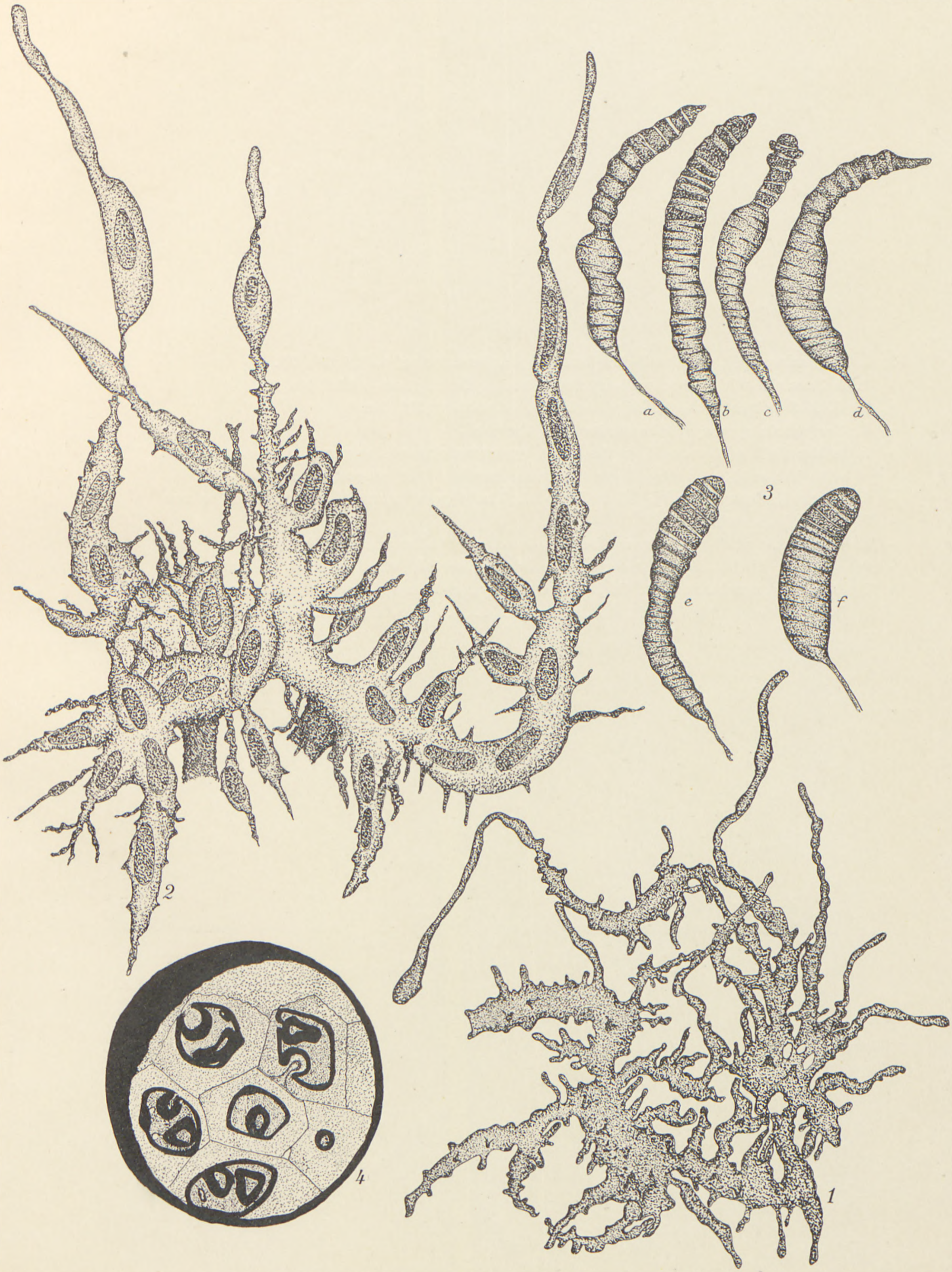

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Plate III.

Fig. 1. A *Succinea* wiith six well-developed sacks. Description p. 124. No. 75.
- 2. A *Succinea* with three well-developed sacks. Description p. 122. No. 21.
- 3—5. A *Succinea* with six large sacks. Description p. 119. No. 9.
- 4. The whole sporocyst dissected out of the shell.
- 5. Is the shell of the snail to show the enormous size of the parasite in comparison with the snail, and how large the space is which the parasite occupies.
- 6.–7. A snail drawn on $^{23}/_{3}$ 27 and $^{7}/_{4}$ 27. The figures show the growth of the two sacks in a fortnight.
- 8.–10. The same snail. In 8 drawn before dissection, 9 after the mantle cavity has been opened. In 10 all the viscera have been dissected away, only the genital organs and the parasite remain. Of the five free lying sacks only some have been drawn. Description p. 121. No. 47 . . . . ✕ 6

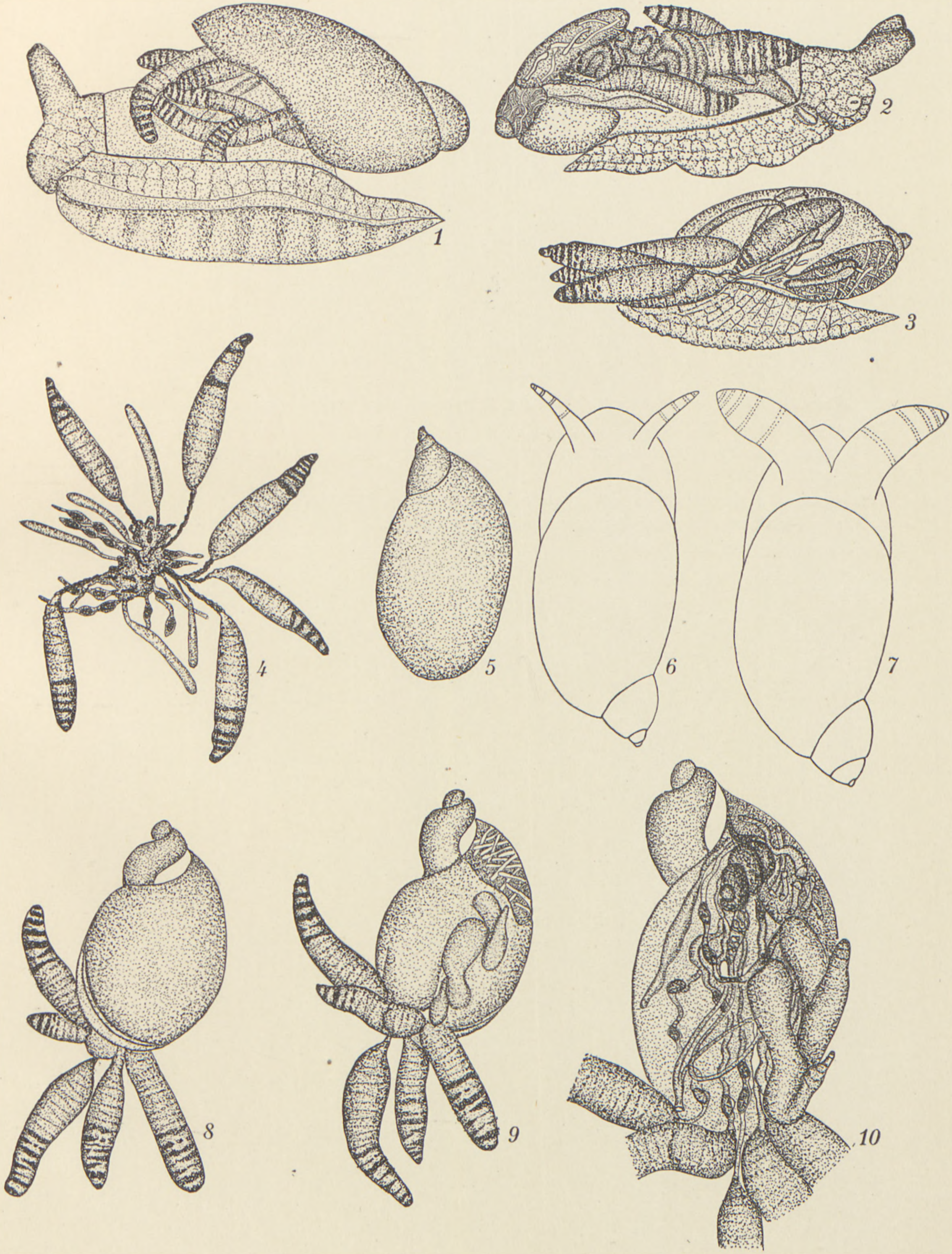

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Plate IV.

Fig. 1.⎱ A snail with two large sacks; in Fig. 2 part of the genital organs are seen.
- 2.⎰ Description p. 119. No. 3.
- 3.⎱ A snail with two large sacks. In Fig. 2 the genital organs are seen. Description
- 4.⎰ p. 121. No. 28.
- 5. A snail with three very irregular sacks. Description p. 123. No. 22.
- 6. A snail with two large sacks. Description p. 118. No. 2.

Figs. 7—8 shows a shell of a *Succinea*, the two sacks, and the genital organs of the snail. . . × 6

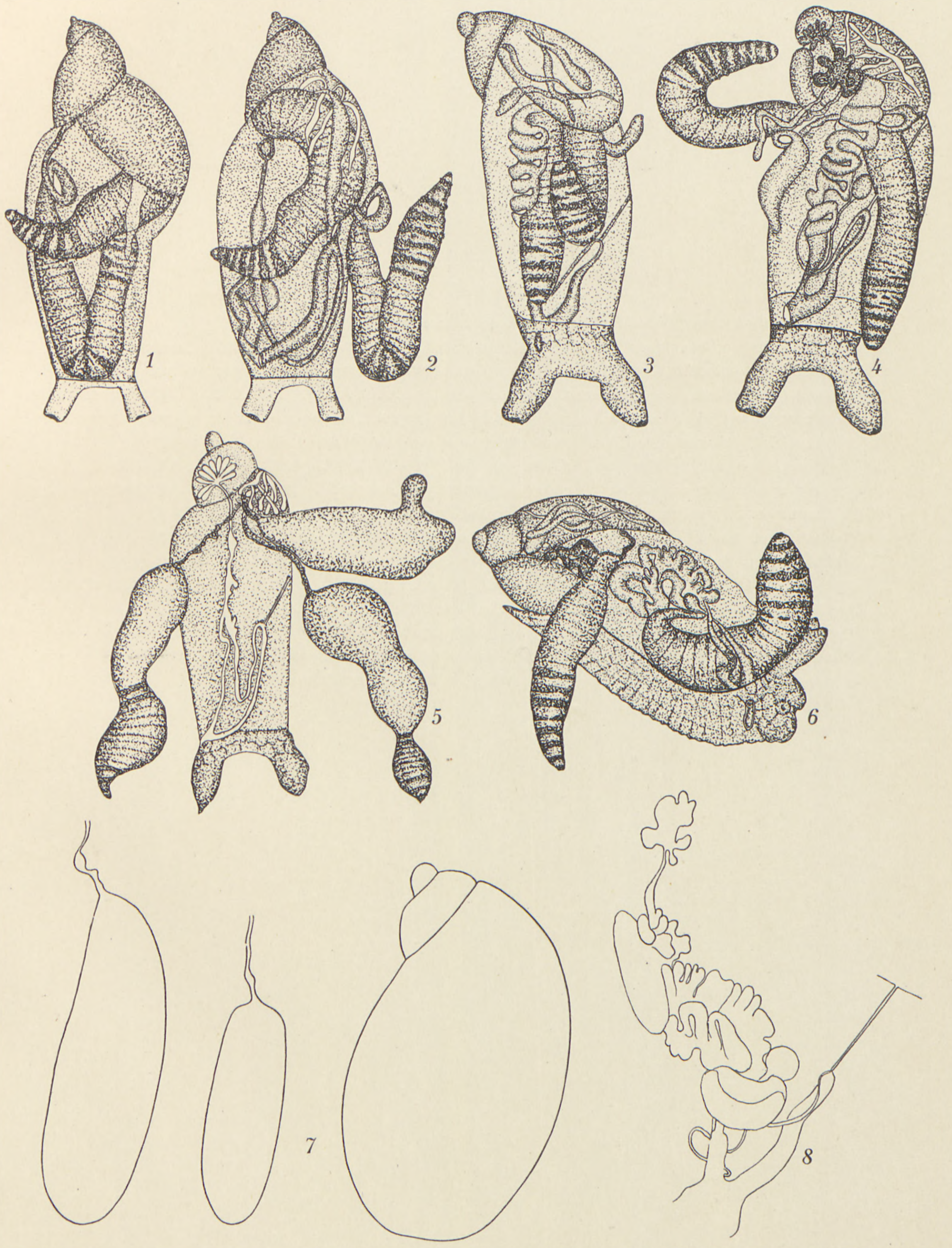

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Plate V.

Fig. 1. Normal genital organs of *Succinea putris*, seen from the inner side.

- 2. The left part of the figure, seen from the outer side. hg. hermaphrodite gland; vd. vesicula seminalis; ab. albumen gland; so. sperm-oviduct; o. oviduct; vd. vas deferens; m. muscle; p. penis; r. c. spermatheca. . . . . a*. Sucherocular
- 3.} A sporocyst with 6 sacks in different stages of development. 4 The shell of the young
- 4.} snail which has contained the enormous parasite. Description p. 120. No. 15.
- 5. The sexual organs of the snail drawn in Figs. 5—7, Pl. VI, p. 121. No. 45. The figure shows how enormously the sexual organs may be reduced by the parasite. . a*. Sucherocular.
- 6. The same sexual organs as figured in Fig. 5, but drawn with a high power (a*. Oc. 4). The albumen gland has almost disappeared and the rest is reduced to mere strings.
- 7. Sexual organs belonging to the snail No. 47 figured on Pl. III, Figs. 8—10 and described p. 121. . . . . 121 a*. Oc. 4
- 8. Snail without large sacks; and some smaller ones. Description p. 120. No. 12.
- 9. The shell which has harboured the enormous parasite.
- 10. The same snail; the sacks are dissected out and the genital organs of the snail are seen. They are almost at the same stage as those figured in figs. 5—6.

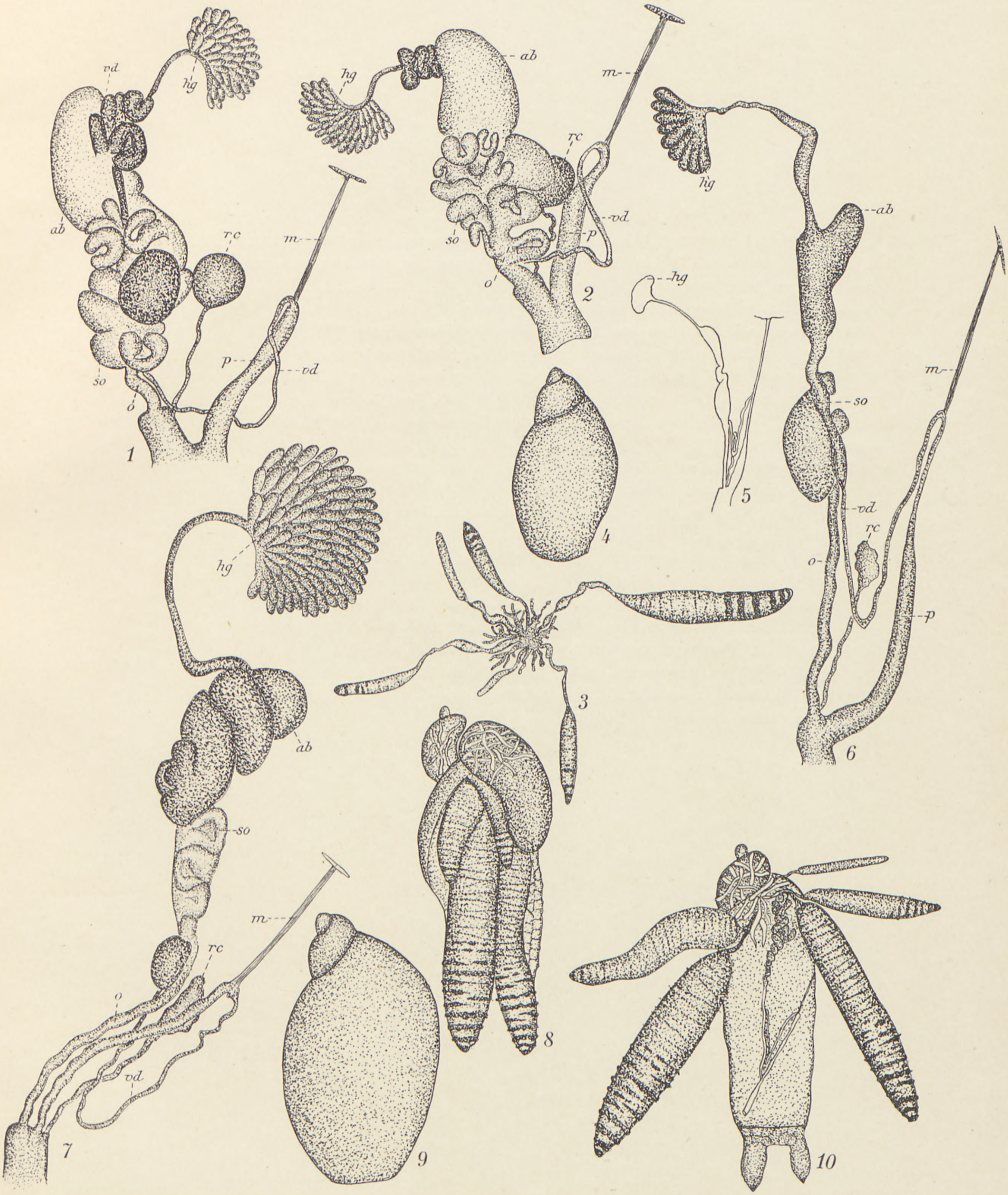
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Plate VI.

Fig. 1. Snail with four sacks and rather well developed sexual organs. Description p. 122. No. 48.

- 2. Liver of the same snail; seen from without. It shows how two long immature sacks are lying on the surface of the liver. *8
- 3. A small snail with two large sacks. Description p. 122 No. 5.
- 4. A small snail with an enormous abnormal sack. Description p. 123. No. 50.
- 5—7. A large snail showing seven sacks all ripe. The three drawings were made during the dissection, Fig. 5 after the snail had just been opened, the genital organs are reproduced in figs. 5—6 on Pl. V. Description p. 121. No. 45.
- 8. A large snail showing one large and two smaller sacks and a lot of smaller ones. Description p. 120. No. 24.
- 9—12. Four sections of a snail to illustrate the causes why one snail has only one large sack and another six or more sacks.

  Fig. 9. Section through a snail not parasitised. Figs. 10—12 sections through parasitised snails.

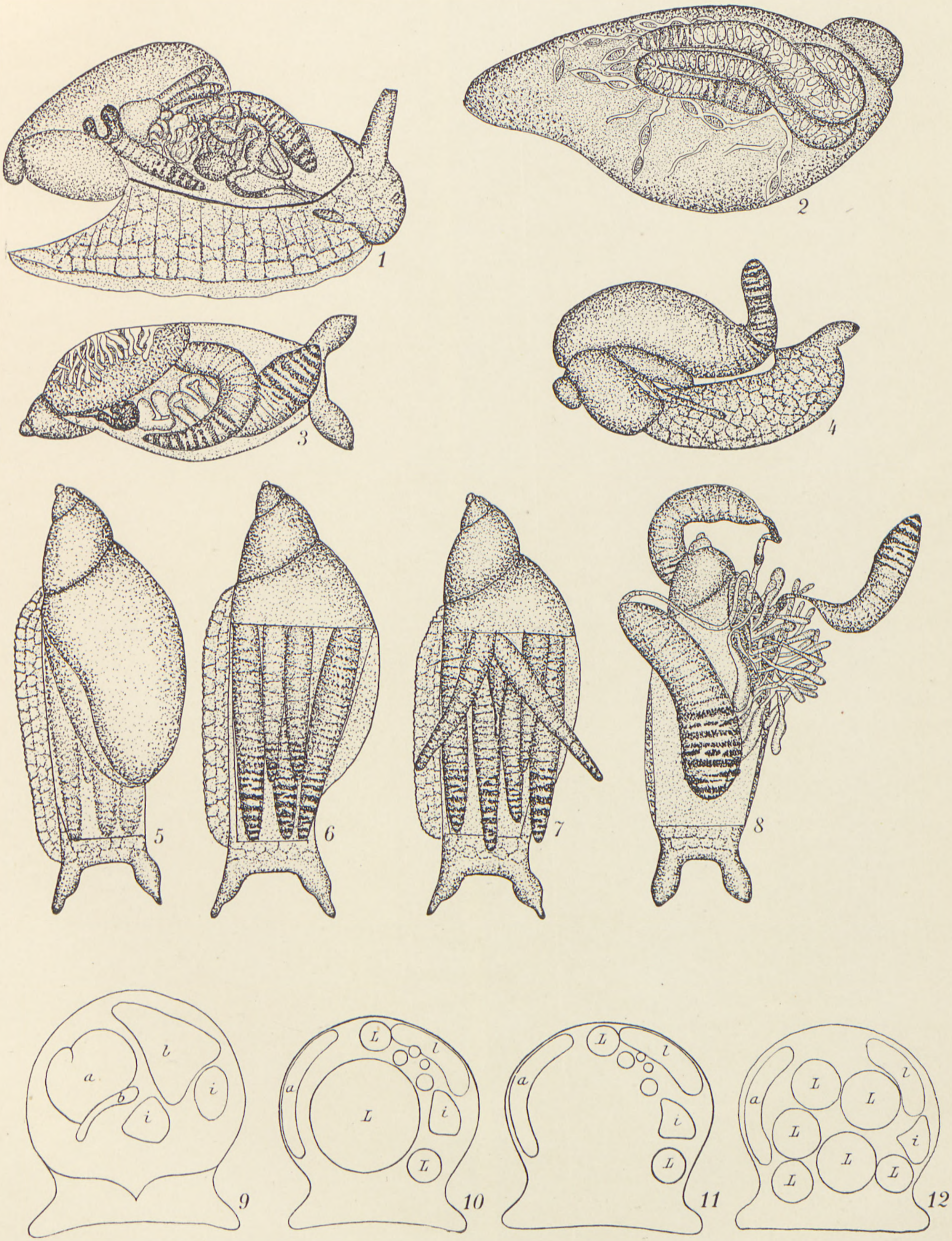
  Fig. 10 shows one large sack and 6 smaller ones of which one is lying below the strongly reduced liver (Fig. 4).

  Fig. 11. Section of a snail which has got rid of the large sack.

  Fig. 12. Section of a snail in which the small sacks in fig. 11 have grown up and occupied the empty space left by the large one (Figs. 5—7).

  Figs. 10—12 are camera drawings from animals fixed in sublimate.

  Fig. 10 corresponds to Fig. 4; Fig. 12 to Fig. 5—7. a-b. Sexual organs; l. Liver; i Intestine. L. sacks.



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