

CONTRIBUTIONS  
TO  
THE BIOLOGY OF THE ROTIFERA

PART II  
THE PERIODICITY AND SEXUAL PERIODS

BY  
C. WESENBERG-LUND

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WITH 15 PLATES AND 8 SCHEMATA

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D. KGL. DANSKE VIDENSK. SELSK. SKRIFTER, NATURVIDENSK. OG MATHEM. AFD., 9. RÆKKE, II. 1.



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HOVEDKOMMISSIONÆR: ANDR. FRED. HØST & SØN, KGL. HOF-BOGHANDEL  
BIANCO LUNOS BOGTRYKKERI A/S

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## Introduction.

From 1892 down to the present year I have studied the biology of the Rotifera, i. e. for more than about 35 years. My researches have mainly been carried out upon material gathered in Nature, and studied in the laboratory immediately after the samples had been taken. I am sure that I can now say that several thousand samples have passed before my eyes. Many of them were included in my Plankton Investigations, and are mentioned in the main part of this work (1904—1908), while very many were taken on excursions on which studies relating to other freshwater organisms were the principal object.

When I began my work in 1892 MAUPAS had just (1890) published his famous short papers in "Comptes rendus"; they were, however, unknown to me for several years. Almost simultaneously LAUTERBORN and myself have tried to elucidate the periodicity of the Rotifera. LAUTERBORN's papers appeared in 1898—1902, just at the time when mine should have been printed. As the results of our researches were almost congruent, I provisionally withdrew most of my publications but I have continued my investigations down to this very day. My explorations have, in ever-increasing degree, aimed at an elucidation of the periodicity, and the sexual problem, and at the discovery of the males which have hitherto been very little known. This latter part of my studies was published in 1923. Now that the part relating to the periodicity, the occurrence of the sexual periods, and the sexual problem is being published, I am well aware that my work in a very high degree bears the stamp of imperfection, partly owing to insufficient knowledge in domains which were originally foreign to me. —

It is a well-known fact that almost all our knowledge of the problem of sex determination in organisms with heterogonic propagation has been built up in the period since 1895; the same is the case with all that we know with regard to the problem of seasonal variation (= temporal variation = cyclomorphoses), furthermore with the cytology and ovogenesis of the Rotifera. It is to the same period that all more thorough investigations relating to the surrounding medium belong, furthermore, the exact studies relating to the annual regular variations in temperature, the chemical composition of the fresh water, and the plancton community, in which the rotifers play such a prominent part. It will therefore be understood that the

enormous amount of scientific facts which have been accumulated during these thirty years, has greatly influenced my explorations. The majority of all these results have been gained far away from my area of work, in the laboratories; many of them have been contradictory and are so to this day. For a long time it seemed as if students in the laboratory again and again arrived at results which were incompatible with those gained by work carried out in Nature. Year after year my explorations gave the same results; the interpretations might be wrong, the results could not. Owing to the self-confidence very often characterizing workers in the laboratory and to which the labourers in Nature are only rarely able to rise, it was long the custom to underrate the results gained by explorations in Nature. During the last few years, however, it has been understood that this was not the right way to progress, and workers in the laboratories have tried to bring about congruity between the studies in the laboratories and those in Nature.

The main results of the laboratory-studies have, I believe, been the pointing out of very many and very valuable small facts elucidating the sexual biology of the Rotifera, and, in addition, the furnishing of a highly needed foundation for the suppositions, thoughts and theories which the work in Nature had occasioned. All in all I cannot see that these studies have been productive of results which, with regard to their significance, have overshadowed MAUPAS' fundamental explorations with which the period was inaugurated. I have thought it best in the following to try to give in one chapter, first the main results of all papers relating to the sex determination and cyclomorphoses in brief summaries, and then to sum up in short sentences the main results of the whole of the laboratory work from MAUPAS to our day. Then follows my own work; finally I shall try to combine the results from the two different lines of investigation; in the summaries I have partly used the authors' own words. —

As is generally known, LAUTERBORN, and later on W-L, had arrived at the result that the Rotifera, just as the Cladocera, could be divided into polycyclic, dicyclic, and monocyclic species; many colonies, living pelagically in larger lakes, could most probably be regarded as acyclic. The different species had their distinct sexual periods, at quite distinct seasons of the year; the sexual periods were inaugurated by high maxima, after which the males appeared. Beyond these periods these males did not appear or were at all events extremely rare. LAUTERBORN (1898 p. 182) arrives at the following main results:

“Das Auftreten von Männchen und damit die Bildung befruchteter Dauereier ist an bestimmte Generationen gebunden. Ich stelle mir vor, dass die aus den Dauereiern ausschüpfenden Weibchen die Fähigkeit besitzen, sich durch eine Reihe von Generationen hindurch auf parthenogenetischem Wege fortzupflanzen; nach einer gewissen, von den Existenzbedingungen der einzelnen Arten abhängiger verschiedenen Zahl parthenogenetischer Generationen erlischt allmählich die Fähigkeit der ungeschlechtlichen Reproduktion, und es stellt sich ein Befruchtungsbedürfnis ein, vergleichbar etwa dem Kopulationsbedürfnis der Infusorien nach einer langen Reihe ungeschlechtlicher Teilungen. Dieser Befruchtungsbedürfnis äussert sich darin,

dass an Stelle der grösseren Sommereier zahlreiche Männcheneier auftreten, die befruchtet zu Dauereiern werden."

LAUTERBORN expressly maintains that internal conditions govern the cyclus, but simultaneously he says that also external conditions, such as the composition of the fresh water, may have an indirect influence which is supposed to be especially conspicuous in the case of the monocyclic Rotifera. —

With regard to the main results I entirely agreed with LAUTERBORN, and having now studied the males for thirty years I still do so. I am fully convinced that the assertion that the colonies of the different species of the Rotifera in the different localities have their sexual periods at distinct times of the year, is correct. On the other hand, with regard to the theoretical explanation of the phenomena I am not aware that I have anywhere expressed any opinion as to whether the phenomena are the results of external or internal conditions. Nevertheless, it has often been maintained that on that point too, I have fully supported LAUTERBORN. —

In reality this has not been the case. As is generally known, I have tried to explain the seasonal variations especially in the Cladocera as accommodations to the regular variations in specific gravity and viscosity of the fresh water i. e. in the external medium.

He who has studied the regular variations in temperature, viscosity, light, and amount of plancton recurring year after year, will always be most inclined to suppose that the presumed regular variations in internal conditions, causing the variations in propagation, are in some way connected with and partly dependent upon these factors, which govern all organic life and its modes of expression.

All later explorers have corroborated the view that the seasonal variations mainly assert themselves at the temperature 14—16° C., and that a series of plancton organisms, especially many plancton Cladocera, have another and greater power of buoyancy in May—June than in February-March. Now, it can be shown that it is just at the same temperature and in the same season of the year that the great variations in propagation, the appearance of males among the Cladocera and of mictic females among the Rotifera, very often take place. Hence it will no doubt be understood that a onesided maintenance of the theory that variations in internal conditions should cause the variations in propagation would be very unnatural, I may perhaps say quite illogical.

It is a well-known fact that the greater part of all our knowledge with regard to sex determination in the Rotifera has been built up upon studies of one single species, namely *Hydatina senta*. During the last few years other species, too, especially those of the genus *Asplanchna* have been used. On the other hand, those who have studied the problems connected with propagation in Nature have never used *Hydatina* but many other rotifers, especially plancton-rotifers which the experimenters in the laboratories have not used, and, as far I can see, are only able to use with the greatest difficulty.

We know much more of the life history of *Hydatina senta* than of any other rotifer, but all our knowledge is acquired in the laboratories; of its life in Nature we know hardly anything. According to COHN (1856) *Hydatina* seems to be dicyclic with one sexual period in April and one in September. WEBER (1888 p. 676) has also observed a sexual period in the spring.

These results were not in harmony with those arrived at by MAUPAS' and NUSSBAUM's studies in the laboratory, and LAUTERBORN (1898 p. 181) therefore quite correctly maintains that the life cycle of *Hydatina* is not in accordance with that of the plancton rotifers. Furthermore he has correctly observed that *Hydatina* lives in *Euglena* and *Chlamydomonas* pools, very small areas of water which are of an ephemeral nature and often dry up. The results at which MAUPAS and NUSSBAUM have arrived, namely that rising temperature and insufficient nourishment should be male-producing factors, may be quite correct just for this species, whereas it is highly improbable that these two factors should be of significance for all those rotifers which inhabit perennial areas of water.

It would therefore be of interest to know the life cycle of *Hydatina senta* in Nature; having overlooked the above-mentioned remarks of LAUTERBORN with regard to habitat, I long searched in vain for *Hydatina*; but after finding it, I have studied its life cycle in Nature for three years and in several localities. —

On the plates I have figured those rotifers whose anatomical features have been insufficiently known; in addition they illustrate some biological traits, especially with regard to the deposition of eggs of the plancton organisms, furthermore the male of *Asplanchnopus*, not found when Part I of the work was published.

The plates have all been drawn by myself, with a camera and from living animals, they only show what may be seen without staining. My assistant, Mr. BERG, has helped me with the shading of many of the figures.

On plate I is shown a *Rhinops vitrea* female; I hope that, keeping the numbers of this figure in mind, the reader will be able to understand the anatomical details in the other figures. —

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## Chapter I.

### The Literature relating to Sex Determination and Seasonal Variation among the Rotifera.

#### a. Sex Determination.

As is generally known, MAUPAS was the first who tried to solve the question relating to the sex-determination of the Rotifera: he arrived at the result that temperature was the sex-determining factor; high temperatures augmented the production of mictic females, low temperatures that of amictic ones. MAUPAS further-



more maintained that the temperature is only able to influence the determination of the sex if its influence coincides with the beginning of ovogenesis; later on it has no influence. "Ni la nourriture ni le temps, ni la lumière, ni la température elle-même rien n'y fera plus." (1891 p. 2).

None of the many later experimenters have been able to confirm this view. In fact, outdoor explorations clearly show that the appearance of "epidemics" of males and the rise of temperature coincide in very many cases, but this ought not to be understood to mean that it is the rising temperature which directly influences the production of males. From a long series of experiments NUSSBAUM (1897 p. 227) arrived at the result that it was the nutriment which determined the appearance of mictic or amictic females. If a newly born female is well nourished till the appearance of the first egg, it will produce amictic females during the whole of its lifetime, if badly nourished, it will produce mictic ones. Before and after this period neither nourishment nor temperature has any influence upon the determination of the sex. The influence of the temperature is only an indirect one. This result has again been severely criticised by almost all the following authors.

PUNNET (1906 p. 223) arrives at the result that neither temperature nor nutriment can be said to have any sex-determining influence. He avoids the necessity of having recourse to external influences, he supposes that it may be a characteristic of certain ♀ to produce mictic females and of others to produce none. From his experiments he arrives at the result that there are definite sex strains. Some strains (A) produce 40 to 50 per cent of males, others (B) produce a very low percentage, 2 to 5 per cent, while others again (C) produce no males at all, although reared through as many as seventy-three generations. Most of the females belong to the category B. Neither temperature nor nourishment, it is stated, are able to exercise any sex-determining influence upon these strains. The sex-determining factor is internal: zygotic constitution. He admits, however, that these different zygotic constitutions may perhaps be modified by external conditions, though he himself did not determine the cause of such modification.

Now the American authors begin their admirable explorations inaugurated by WHITNEY. All these explorations clearly show that variations in the external medium at all events have some influence upon sex-determination.

In his paper (1907 p. 1). WHITNEY like PUNNET maintains that temperature and nourishment have no direct influence on the determination of sex in *H. senta*; indirectly they determine the number of each sex produced, regulating the number of eggs that each kind of female lays. At a temperature of 20—22° C. the mictic and amictic females lay about the same number of eggs each, at a temperature of 26—29° C. the mictic females lay about four times as many as the amictic females. He further shows that the mictic females occur in the early part of a family of daughter females, and that starving of the young females for the first few hours after they hatch does not cause them to produce a higher percentage of male eggs. He finally shows that the three strains of PUNNET can be found in one strain, and

that each is capable of giving rise to the other types, according as the data are scanty or extensive. According to WHITNEY there are therefore no strains that constantly produce a high or a low percentage of mictic females. A strain only producing amictic females does not exist. With this paper almost all that the European authors had built up was broken down again. In 1908 b WHITNEY (p. 137) shows that there is probably a reduction in the number of chromosomes in the male parthenogenetic egg and in the winter egg, but not in the female parthenogenetic egg (See also LENSSEN 1898). It is not in itself the reduction of the number of chromosomes and the formation of the second polar body which determine the ultimate sex of the egg; on the other hand, as in the resting egg which becomes fertilized as well as in the parthenogenetic egg from which a male is hatched, there is a reduction in the number of chromosomes during maturation, the conclusion seems permissible that the sex of the embryo in the male egg is changed by the entrance of the spermatozoon. —

In a series of very suggestive papers SHULL has again tried to find out the influence of the various agents which are supposed to affect the proportion of mictic females. His main result (1910, p. 344) is that none of the hitherto supposed agents has a direct influence on the proportion of mictic females. Sex determination is dependent upon external as well as internal factors. He comes to the result that there really exists a factor in external conditions which not only accounts for the results of the present experiments, but affords a simple probable explanation of the result upon which the previous contradictory conclusions were based. This factor is supposed to be the chemico-physical composition of the medium in which the animals live, especially certain substances dissolved in the water in which the rotifers are reared; these substances may exert a potent influence on the proportion of mictic females; according to SHULL the accumulation of substances in old cultures may be responsible for almost all the results at which all previous authors as well as he himself have arrived upon this subject; if the progeny of the last daughters in a family produces a smaller number of mictic females than the first one, this is due to accumulation of substances in the culture, arisen during the nourishment of the organism. Among many other interesting points SHULL's studies have, however, especially elucidated the following fact. WHITNEY had found that mictic females occurred in the first two-thirds of their respective families; at high temperatures shorter families were produced than at a low temperature. If these families were curtailed by cutting of the last members which were nearly all amictic, the percentage of mictic ones would be increased. Now SHULL in contradistinction to WHITNEY shows that mictic females are not accumulated at either end of a family whether this family is large or small. A short family is not a curtailed long family; it is built on a plan of its own, which is approximately the same, relative to its length, as that of a large family. Like WHITNEY and in contradistinction to PUNNET SHULL maintains that sex strains have not been observed. The strains of PUNNET are artificial products, caused by different nourishment.

Simultaneously SHULL pays attention to the fact that internal factors may also have exerted their influence.

The next question was: What are the substances which influence the production of mictic females? In a later paper (1910 p. 345) WHITNEY now ranges himself on the side of those who hold external factors accountable for all variations in the percentage of sexual forms, male production being favoured by the presence of some substances in solution, the nature of which is undetermined, but the absence of which predisposed to the production of amictic females. He maintains that in horse manure there exists a factor which causes the production of mictic females; if this factor is wanting, the amictic females produce only amictic ones.

In his next paper SHULL (1911 a p. 117) tries to find out some of those chemical agencies which according to him may exert a potent influence on the proportion of male producers. His main results are, as previously, that both external and internal agents are involved in the production of the life cycle. With regard to temperature it seems that it really may have some influence, but this may only be an indirect one inasmuch as the response of the rotifers to both external and internal conditions may be modified by temperature. More effective than temperature in modifying the proportion of male producers are certain chemical substances. Horse manure, urea, beef extract, and creatin solutions all greatly reduce the proportion of mictic females. A higher degree of alkalinity seems to do the same. WHITNEY (1910) and SHULL (1910 and 1911) agree with each other that chemical substances are responsible for the effect upon the life cycle. But whereas SHULL has shown that it is certain substances present in the manure solution which prevent the mictic females from appearing, WHITNEY (1910 p. 348) believes that it is a certain substance present which causes the mictic females to appear, and that it is only when this substance is absent that amictic females alone occur. This chemical substance, which is not more precisely indicated, may be a transitory one.

With regard to internal factors SHULL (1911 a, p. 164) further shows that pure lines obtained from widely separated localities were found to yield a constantly different proportion of male producers even though external conditions were the same for both. If a member of one of these pure lines was mated with a member of the other pure line, pure lines appeared having in every case a higher proportion of mictic females than had either parent pure line.

In 1912 (p. 283) SHULL continues his studies on the internal factors and shows that long continued parthenogenesis in some lines of *Hydatina* causes a decrease in the proportion of mictic females, and he supposes that this decrease may partly be responsible for differences observed between parthenogenetic lines in cases where the ages of lines are unknown. SHULL further shows that the period in which it is decided whether a female is to be mictic or amictic is always the growth period of the parthenogenetic egg from which the female hatches. Microscopical examination of the living animals shows that the last few hours of the egg-stage within the parent's body includes the entire growth period. Before these last hours of the egg-

stage, manure solution is able to reverse the sex determination of the egg, after this period manure solution is not able to do so. It will be understood that sex is determined a generation in advance. As a result of these observations it may also be mentioned that individuals hatching from fertilised eggs are not only all females but also amictic ones, as ascertained from 469 hatchings from resting-eggs. As far as I understand, ZAWADOWSKY (1916) has arrived at a very similar result (*Diglena volvocicola*). In a paper which I have not been able to procure (1912 a) WHITNEY has arrived at the following result with regard to strains: The parthenogenetic races may differ from each other either in their power of producing amictic females or in their power of reaction against factors which influence to the production of mictic females. WHITNEY supposes that it is the last alternative which is the most correct. —

WHITNEY (1912 b p. 337) shows that races of *Hydatina senta* which were allowed to reproduce parthenogenetically for 384 generations, extending through a period of twenty-nine months in identical environment, present a gradual decrease in their rates of reproduction. In the one race only one female out of the sixty isolated was able to live and reproduce, while twenty others lived the normal length of time for individuals of the race, but never laid any eggs. These twenty females developed and produced many eggs in their ovaries but never laid them. The eggs remained inside the body and ultimately seemed to fill the entire animal; some of the eggs started development into embryos but they died and many of the egg-membranes ruptured, and the body of the females became filled with a mass of egg-material from the broken and decomposing eggs. These sterile females became larger than normal females. Another race had lived through 503 generations and was still living when the paper was published; it was now in a very exhausted condition. WHITNEY further shows that cross-fertilisation of two weakened races greatly reinvigorates both races and is probably able to restore them to their normal vigour which they possessed when they started from the original fertilised eggs.

SHULL (1915 a p. 145 and 1915 b p. 187) discusses the periodicity in the reproduction of males in *Hydatina senta*. He shows that there is a well-marked rhythm in the production of males in *Hydatina senta*; MITCHELL (1913 a, b) has found the same in *Asplanchna amphora*. Because the intervals between the periods of many males is quite regular in some lines, and not the same in all lines reared simultaneously, SHULL supposes that this periodicity is due to an internal factor. In well-nourished lines there is some doubt whether there was any correlation between size of family and number of mictic females. In starved families, on the other hand, the greatest numbers of mictic females were not in the largest, but in those of medium size. On the statistical evidence as a whole the influence of quantity of nutrition upon male production is held to be "not proven". When qualitative differences in nutrition affect male production, the interval between periods of many males probably remains unchanged.

In 1915 (a) SHULL shows that races of rotifers might differ very largely in the

place of egg-laying. One race laid its eggs very largely on the bottom or sides of the dishes; another race chiefly attached them to the surface film of the water.

In 1916 SHULL and LADOFF further discuss the factors affecting male production in *Hydatina*. The main result (according to WHITNEY 1917 p. 101) is that an excess of oxygen in the culture water may cause a greater production of mictic females than in experiments without an excess of oxygen.

In four consecutive papers WHITNEY shows the influence of food in controlling sex in *Hydatina* (1914 a p. 832, 1914 b p. 545, 1916 a p. 263 and 1917 p. 101).

In the papers 1914 a and b WHITNEY shows that rotifers fed upon a green organism *Chlamydomonas* produced many more mictic females than those fed upon the usual colourlers *Polytoma*.

In 1916 (a) WHITNEY shows that in five different species of rotifers the production of mictic and amictic females may be regulated at will by certain manipulations of the food supplies. In this as well as in the earlier paper 1914 WHITNEY changes his view, ascribing to variation in the quantity of food supply a greater rôle than formerly. In some species a continuous diet of a colourless flagellate *Polytoma* caused only amictic females to be produced, whereas when it was replaced by a green flagellate *Chlamydomonas*, nearly only mictic females appeared. When one of the species had only a scanty diet of *Chlamydomonas*, only or nearly only amictic females appeared, whereas a more abundant diet of the same pure cultures of *Chlamydomonas* caused as much as 90 per cent of mictic females to be produced. HODGKINSON arrived at a very similar result (1918 p. 187). In 1917 WHITNEY further shows that four other rotifers *Brachionus militaris*, *Brachionus Bakeri*, *Euchlanis dilatata* and *Brachionus Mülleri*, when the green food supply of *Chlamydomonas* was made very abundant, produced a high percentage of mictic daughters, whereas, when the green food supply was allowed to become scanty, very few, if any, mictic females were produced. WHITNEY further shows that the results at which SHULL and LADOFF arrived may be interpreted in another way than these authors have thought. An excess of oxygen in the culture water does not directly affect a mother and cause her to produce mictic females, but by affecting the conditions that influence an increase or a decrease of the micro-organisms which constitute the food supply, it may indirectly cause her to produce either mictic or amictic females. Oxygen usually favours an increase in the number of bacteria in the cultures, but if too many bacteria are produced, they or their products interfere with the normal metabolism and reproduction of the rotifers. If, on the contrary, a sufficient number of bacteria are not maintained in the culture waters, the rotifers are deprived of more or less of their food supply. All kinds of bacteria in these conglomerate mixtures are not in the same way useful to the rotifers, and it may be supposed that, as there are so many millions of individuals in a watch glass at the beginning of the experiment, it is a matter of chance which species will survive and maintain itself, or will even increase its own numbers. In some cultures those species of bacteria which

cause favourable food conditions, producing mictic females, will be developed, in others these will not be developed, and amictic females will appear.

In a paper (1918 a p. 521) SHULL continued the explorations of SHULL and LADOFF (1916) and showed firstly that an excess of dissolved oxygen, in which the excess was obtained by saturating the water with an atmosphere of which 60 p. c. was oxygen, really as supposed in 1916, is a male-producing agent. Now, however, it was further shown that whether the excess of oxygen was obtained from a 40 p. c. oxygen atmosphere or from a 60 p. c. one, the increased male production was almost the same; the lower concentration is perhaps indicated as being a little more effective in inducing male production. This result was contrary to WHITNEY'S, which seems to be based on the supposition that, if oxygen were a male producing agent, the more oxygen there was present, the more males there should be. SHULL further criticised WHITNEY'S above-named results, that green organisms as food increase the production of male producers; the result of WHITNEY'S explorations are by no means denied, it is only maintained that all the factors obviously associated with *Chlamydomonas* in the cultures should be separately tested before any residue of influence is assigned to nutrition. SHULL now compared cultures, in which *Euglena* was used as food, with cultures in which manure scum was used as food, and it was shown that under the experimental conditions the first-named contained on an average about 62 p. c. more oxygen than the manure scum cultures. When therefore *Euglena* increases male production in *Hydatina*, as much of that increase is presumably due to oxygen as is directly produced by saturation with a 40 p. c. oxygen atmosphere. Deducting the increase in male production presumably due to liberated oxygen, it was then found that *Euglena* was two or three times as effective as the oxygen, and in one case many times as effective. SHULL further continues his observations with regard to the differences in the egg laying process in different races, and shows that, if the dishes were placed in an atmosphere containing an excess of oxygen, this caused the eggs to be laid more largely on the bottom than when the dishes were kept in air. However, the experiments further show that upon this point, too, there are racial differences, and that it is therefore difficult to judge of the relative effect of oxygen upon them.

In 1919 WHITNEY continued his observations relating to oxygen as a producer of mictic females. Whereas SHULL and LADOFF (1916) and SHULL (1918 a) arrived at the main result that a sufficient amount of dissolved oxygen in the culture water will cause an increase in the production of males, WHITNEY (1917 p. 101) and again in (1919 p. 469) maintains that oxygen only influences the food supply which in turn affects the production of males; the production of mictic females does not depend directly upon the presence of appreciable quantities of free oxygen in the culture water. He criticises SHULL'S experiments and adds as a new fact the following: In the sunlight fewer male rotifers and also fewer mictic females are produced in culture water containing *Chlamydomonas* which have given off much free oxygen, than are produced in darkness in culture containing less free oxygen. These results

are contradictory to earlier ones, but WHITNEY would have them understood to mean that in the sunlight the *Chlamydomonas* become less available as food for the rotifers.

In 1921 SHULL showed that the number of chromosomes is the same in both types of females.

In a very suggestive paper SHULL (1922 a) has studied the relative nuclear volume and the life-cycle of *Hydatina senta*. As is well known, HERTWIG and with him ISSAKOWITSCH concluded that in the life-cycle of parthenogenetic animals the change from the parthenogenetic to the sexual mode of reproduction is a direct result of an increase of the Kernplasma relation. For HERTWIG had conceived the idea that any increase of the quotient K/P would lead to the production of males, decrease of that quotient favouring females. K/P is least in the early generations descended from the fertilised egg. With continued parthenogenesis and favourable conditions the ratio increases, the volume of the nucleus increasing relatively more than the volume of the cytosome. Low temperatures and deficient nutrition hasten the increase. When a given high value of the ratio K/P is reached, males are produced. With a further slight increase in the ratio, sexual eggs are formed by the fusion of groups of oögonia, and in this fusion the Kernplasma relation is reduced. From the life history of *Hydatina* SHULL now supposes that there may at least be three independent ways in which the Kernplasma relation may be connected with changes in the life-cycle, if HERTWIG's views are correct. Firstly, periods of many mictic females may alternate with longer periods of few. The ratio K/P is supposed to change with these alternating periods. Secondly, male production is related to the age of the parents. The first eggs laid by a female yield relatively few mictic females; then they increase gradually up to the middle of the family, then they become gradually less frequent to the end of the family. There should be a corresponding change of the Kernplasma relation during the life-time of the parent. Third, external agents profoundly alter the number of the mictic females. Manure solution may easily exclude mictic females altogether. Animals reared in manure solution should therefore show a different Kernplasma relation from those reared in spring water.

SHULL now shows that, in the relative nuclear volume of the yolk gland of *Hydatina senta* for each of nineteen generations including two well-marked periods of male production, it is difficult to see any relation between nuclear volume and the number of mictic females. SHULL arrives at quite the same result with regard to nuclear volume and age of individual and further to the effects of manure solution. Lastly SHULL shows that, when amictic females and mictic ones from the same families reared under the same conditions are compared with respect to relative nuclear volume, nothing in the measurements indicates that the nuclei of one of these types of female are significantly larger than those of the other type in any of the tissues studied. No conspicuous differences with regard to K/P can be pointed out between mictic and amictic females. The relative nuclear volume in the

yolk gland, stomach, intestine and oöcytes is probably the same in mictic and amictic females.

In the time 1912—1914 the excellent studies by POWERS and MITCHELL on the polymorphism, sex determination and transmission through the resting egg of experimentally induced characters in *Asplanchna amphora*, appeared. Most probably this rotifer was better fitted for experimental work than *Hydatina senta*; at all events it seemed that the results gained with regard to the first-named species were in some respects much clearer and of the greatest significance for the whole question relating to sex determination. Firstly POWERS (1912) showed that there exists, in *Asplanchna amphora*, a peculiar polymorphism, already mentioned by DADAY (1888 p. 140) and later on found again but misinterpreted by myself (1898 p. 200). The main results of the explorations are the following.

From the resting egg there is always hatched the so-called saccate form with 20—40 vibratile tags and a very large contractile vesicle; it is characterised by a high parthenogenetic propagation containing simultaneously eight to nine young ones. In the course of a few days, in cultures as well as in Nature, there is hatched from this form the so-called humped form characterised by two smaller or larger lateral humps; it has 40—60 vibratile tags and a contractile vesicle not so large as in the saccate form. In ponds which have received water only a few days ago, or in cultures which have just begun, only the saccate form appears, but in the course of a few days, from four to fourteen days, only humped forms occur. The humped form gives rise to only one young one at a time; between the two forms there are few intermediate stages. In cultures, when degenerated, the humped form reverts to the saccate form. The humped form is able to live for five months in cultures, but in Nature every heavy shower, after having diluted the medium, will kill the whole colony, and new individuals, invariably of the saccate form, will again be hatched from resting eggs. The entire population of a teeming *Asplanchna* pond readily changes from the saccate to the humped type in one week. At a certain point of time, in cultures as well as in Nature, when the colonies have grown very large and enormous amounts of individuals are crowded together, there appears a third form the campanulate one, a real giant, 2—2½ mm, among the rotifers; it differs with regard to form of corona, trophi and number of vibratile tags (80—115). The form is a result of cannibalism and also appears when the colony is fed with special food organisms especially *Moina*. In Nature, too, it has been shown that, after the appearance of enormous amounts of young *Moina*'s, the campanulate form appeared from the humped one, only rarely directly from the saccate type. Very often the humped form was eaten up by the voracious, campanulate form. The first individuals appear with the utmost suddenness, and all in all transitional periods are brief. The trophi in every case indicated a complete and sudden transition from the campanulate to the smaller humped type. During the time in which the change took place, the whole colony was in a truly chaotic condition; the campanulate forms produce partly the humped, partly their own



form. Of the three forms there are again special forms; one of the humped forms with very long slender humps is especially interesting, deriving from a combination of overfed parents and foodless progeny. The males which only live two to four days are produced by all three forms of females, but only in slight numbers of the saccate form. POWERS regards the species *A. amphora* as distinct from *A. Brightwelli*, but states that in a single locality he found an *Asplanchna* which in every external character seemed to be *A. Brightwelli*; a closer examination showed that the trophi had a strong inner tooth as in *A. amphora*; they were cultivated in many cultures, hatched from resting eggs, but persistently gave always the amphora-type. Besides, the specimens were typical *A. Brightwelli*; in the very large amount of material the specimens of the campanulate form appeared, but never humped forms. In this connection it is of great interest to remember that later on MITCHELL and POWERS (1914 p. 394) in some of their cultures got a number of males, among which a number appeared like transitional forms between the males of *A. amphora* and *A. Brightwelli*.

The experimental work connected with the elucidation of those external and internal conditions which might produce these different forms, was carried on by MITCHELL (1913 a). He first showed that in mass cultures the saccate forms derived from resting eggs in about six days, but already in the course of only about 10—12 days the entire culture had changed to the humped form. On the other hand, when reared under uniform conditions, the saccate form reproduces its own type indefinitely; it is only in mass cultures that the humped type appears, not when the saccates are cultivated in pedigree series. When some saccates from these cultures were allowed to reproduce in mass cultures, transition to the humped forms occurred. This indicated the possibility that a tendency towards the mutation-like change is inherent in all individuals, although the presence of some unfavourable condition or the absence of some necessary stimulus may in some way suppress it. In the hope of finding a clue to some external or internal factor, plots were made of some of the experimental series, and resultant curves were drawn. The curves demonstrated a marked rhythm in reproduction, showing certain periods or generations in which the rotifer is in a higher physiological state than others. It was then supposed that this rhythm would be one of the factors causing the transition from the saccate to the humped form, but it was shown that this factor was not able to produce this transition; also between the earlier and later individuals produced by a single parent no difference could commonly be found; also the size of the parent in lines with common ancestry and without mutation did not directly influence the size of the offspring. It was further shown that neither change in temperature in itself, nor starvation of the saccate type, nor alternate feeding and starvation in isolation cultures caused mutation.

Having used the cultures for three and a half months, and, obtaining, in some instances, nearly forty generations without a single transition to the humped form, it was thought that possibly the strain of rotifer used was unsatisfactory, due

either to initial weakness or other causes. New lines were started from eggs freshly collected in January from borders of ponds where it was known that the species had flourished, and that at least a portion of eggs had been subject to both freezing and drought. Pedigree series from this material were fed with *Paramecium* and then replaced by *Oxytricha*. Having ignored the new food at first, the digestive tracts remained empty, and no young were produced in the generation thus fed for a period of three days. On the fourth they suddenly began to gorge themselves with *Oxytricha*; a saccate individual was born in the direct line, followed by individuals transitional towards the humped type. The young were likewise fed on *Oxytricha*, and they in turn produced young of the full humped type. The experiment indicated the possibility of qualitative changes in nutrition as a factor determining the sudden transition in type. — Further explorations showed that, when replacing *Oxytricha* by *Euglena*, the transition from saccate to humped followed in the next generation. Further on, if in the old series which at that time had shown an unbroken succession of about sixty generations of the pure saccate type, two sisters were taken out and *Euglena* was given to the one and the customary *Paramecium* diet to the other, it was shown that the first immediately responded by the next generation being of the humped form, the other by the next generation being of the saccate. Lastly it was shown, that, when the lines returned to *Paramecium* diet, within one to four generations all had returned to the saccate type. — The result of the experiments is that a change in food organism or a qualitative nutritional difference constitutes the major factor instrumental in producing the sudden changes. All other factors turn out negative, or at least negligible, in results, as compared to food change.

In a third paper MITCHELL (1914 b p. 225) has tried to find out the sex determining factors in *Asplanchna amphora*. Having given a short resumé of the explorations of SHULL, WHITNEY and PUNNET, he shows with regard to *Asplanchna* that male production is a phenomenon which is all but wholly under nutritive control. Temperature within fairly wide limits is essentially a negative factor in regard to sex determination. He returns partly to the old supposition of NUSSBAUM and that of WHITNEY with regard to *Hydatina*. He shows firstly that continued low nutrition of *A. amphora* reduces male production to zero, and that copious nourishment of the humped type tends to give birth to about 20 p. c. of mictic females. The copious male production is a result of starvation of high potential young females (produced by well-nourished mothers) during the first five hours after birth, whereas starvation of low potential females results in non-male production. MITCHELL further shows that dissolved metabolic products or other substances are not significant factors in male production. Maximum male production is determined by three factors: physiological rhythm, high nutrition, and starvation during the growth period. The first of these influences is one which extends through a number of generations; the second works upon the generation preceding that of the mictic females; the third acts directly upon the male-producing generation itself. Having

discussed and criticised all the works on *Hydatina* MITCHELL calls attention to the general fact that all investigators either used uniform feeding, or at least laid little stress upon qualitative food change; this may possibly be the main cause why the experiments with regard to *Hydatina* gave a negative result. According to him the qualitative variations in nourishment are of greater significance than the quantitative ones. Further MITCHELL points out that if male production depends primarily upon a high state of effective nutrition, it would seem natural that any inhibitory or deleterious substance should limit or prevent the male production.

In their last paper (1914 p. 347) MITCHELL and POWERS have tried to find out if the marked modifications which may be experimentally induced in *A. amphora* are in any sense hereditary beyond the parthenogenetic stages. As the different types may be found bound to different localities in Nature, and as the differences between them seem quite sufficient for specific distinction, the supposition is allowable that we have to do with a species-making process. The essential condition for this supposition is, however, that it has been proved that the variations which produce the different forms at least in some degree influence the sexual gametes. If sexual reproduction always brings the species back to its original form, it is clear that, however varied the parthenogenetic forms are, nothing akin to a new species is formed. As all individuals which hatch from resting eggs are of the small saccate type, and this may be regarded as the most primitive form, it really seems as if it is no species-making process. The question which MITCHELL and POWERS have tried to answer is whether the entire variation of the species, the astonishing variations of the parthenogenetic series, are but a play of the environment upon parthenogenesis as such, or whether they are the result of the forces fundamentally modifying the gametic constitution of the species. Even if the first generation of young hatching from resting eggs is always morphologically the same from whatever type of the species it is derived, there is still the possibility that the young saccate individuals derived from different eggs differ physiologically and in their reproductive tendencies. For it is conceivable that inheritance through the resting egg need not manifest itself in visible characters of the individual which emerges from the egg; it may be hidden as tendencies only to manifest itself in later generations. The main result of a series of admirable experiments is that we have a hereditary transmission of induced germinal modification through sexual as well as through parthenogenetic generations or in other words, that sexual reproduction is unable to wipe out the tendencies induced during parthenogenesis. The main conclusion of the paper is therefore: that the marked morphological changes induced by nutrition are not confined within the bounds of parthenogenetic series only, but as far as the experiments show, are equally transmitted by a sexual process. This renders it at least not improbable that the mutational changes shown in *Asplanchna amphora* are phases of a true species-making process. —

It having now been shown that in all rotifers we have to do with two female forms, the amictic and the mictic ones, it will be understood that it would be of

the greatest interest to take up the whole question for reconsideration, and it is to be hoped that this rare animal will appear again, and that the happy finder may be able to investigate the material thoroughly.

ZAWADOVSKY (1916 p. 1) studied *Diglena volvocicola* and reared them in drops of fluvial water. Like all other observers, he has observed the two sorts of females, amictic and mictic ones. From the moment of its appearance the mother already possesses a well-determined sexual tendency to lay ♀ or ♂ eggs, and only the last-named ones can be fecundated. Sex determination may concentrate its attention not upon the mother but upon the grandmother. The amictic females begin to lay eggs 26—28 hours after hatching, and at intervals of 2—3 hours, (at 20—23° C.). The males are ready to copulate some minutes after having been hatched and after nine hours (with a temperature of 20—23° C. and sufficient nourishment) the females lay one fertilised egg after another. TANNREUTHER (1920 p. 389) has given some valuable observations with regard to the biology of *Asplanchna Ebbesbornii*. It was found in freshly prepared cultures in aquaria in the zoological laboratory in the University of Missouri. It appeared in January and persisted about two weeks, whereupon it disappeared. It reappeared in March, and in May until December 1918, when the paper was completed. In each instance about two months elapsed between the times of its appearance. In each cycle of appearance males, females, and resting eggs were found in about the same proportions. The two kinds of females were observed, furthermore it was noted that fertilisation had no influence upon the amictic form. It is of interest that TANNREUTHER found two sorts of resting eggs, a very thin-shelled one with a single shell membrane, and a thick-shelled egg, with a double shell membrane, the first named develops with the same rapidity as the parthenogenetical, and hatches out immediately after deposition. Two polar bodies are found in each kind of resting eggs (in the parthenogenetical only one) and none of them are developed without fertilisation. POWERS has made the same observation.

The mictic females produced simultaneously or successively males and resting eggs e. g. two resting eggs, one male, one resting egg, one male, one resting egg, one male. — In a female which produces the resting eggs, the yolk spherules become larger and more abundant; the vitellarium becomes darker; the yolk is not produced until at the point where the oviduct takes its origin. The process continues until the vitellarium is completely filled with yolk. Where males and resting eggs are produced by the same parent, the yolk is produced at intervals just before the resting egg begins its growth in the ovary.

In many instances the sperm of the sexually mature male (before birth) would escape from the testis and become deposited in the uterus of the parent, fertilise the mother animal, and bring about the production of resting eggs. The males were rare in the culture; they are very short-lived; they do not increase in size after birth, whereas the females increase to at least four to six times their size at the time of birth. The individuals hatching from the resting eggs are always amictic;

but already the next generation consists of mictic and amictic females. The number of resting eggs in the uterus at any time varies from one to eight. When conditions are favourable, it requires about seventeen hours from the time of the formation of the polar body to the time of birth of the parthenogenetically produced males and females. The males and females are sexually mature at birth. —

In a paper (1922 p. 225) BESSIE NOYES has studied the life history of *Proales decipiens* in cultures. The main results are the following: Twenty-four to thirty-six hours after hatching the animal begins at laboratory temperature to produce eggs. The animal lives about a week egg production ceases on the seventh or eighth day; it is low the first day, reaches its maximum at the fifth, and then declines sharply. In a typical life-cycle an egg deposited by the mother hatches in twelve to twenty-four hours; the embryo reaches the egg-laying period in twenty-four to thirty-six hours after hatching and deposits on the average one egg the first day, three the second, five the third, seven the fourth, three the fifth, one the sixth; death occurs on the seventh day of maturity. The cultures were kept in a solution of malted milk. It could be shown that, whereas during the beginning of the experiments 100 isolated individuals gave an average length of life of 4.65 days, five months later another 100 individuals had an average length of life of 6.17 days. This increase in length of life was accompanied by a marked increase in the number of eggs. It was further shown that under conditions of constant temperature and food the average length of life was lower than the average for individuals kept under conditions of constant food supply and fluctuating temperatures. Six to eight hours before hatching, the embryo in the deposited egg shows movements; the newborn animal moves rapidly and increases in all directions for the first four days, but increases in diameter almost until death. At a certain point a yellow-brown substance begins to appear posteriorly, it increases in amount, the body becomes brownish and the posterior part is inflated; lastly the power of movement is almost lost. If the eggs are laid singly or in lots is not known. It seems as if much more food material is taken in than products are given off, and in the last two days the defecation often wholly ceases. Male eggs have never been seen; amongst more than 50,000 eggs, only sixteen have been found which ought possibly to be regarded as resting eggs. Males have never been seen in the thirteen months in which *Proales* has been under observation. The number of eggs laid every day is not quite constant; if it is high the first day (7 to 9), the life cycle lasts only three to five days; if the number is small (1 to 3), the life-cycle is longer.

As mentioned above, *Proales decipiens* seems to have a wholly parthenogenetic cycle; at all events, for thirteen months males or male eggs do not seem to occur. All those variations in external conditions which SHULL and WHITNEY have tried as male-producing factors have been studied unsuccessfully. In all cases isolations were made for five successive generations, but always with a negative result. It was followed through 250 generations and no evidence of weakening in the race was observed.

It may be added that NOYES has tried to increase the egg deposit and average

length of life through artificial selection, carried out for three months in fifteen generations; the attempt was without avail. She further shows that individuals of a line subjected to the fumes of  $\frac{1}{4}$  and  $\frac{1}{2}$  % ethyl alcohol continuously for nineteen weeks showed a decided reduction in egg-production while under the influence of the alcohol, but their progeny, returned to normal conditions, regain the normal egg producing power after the third generation. —

BIANCO (1924 p. 1) shows, with regard to *Proales felis*, that in all his experiments only parthenogenetic females have appeared.

LITE and WHITNEY (1925 p. 1) have studied the rôle of aeration in the hatching of fertilised eggs of rotifers. It has hitherto been unknown whether a period of inactivity and quiescence is necessary for the normal development of the resting eggs, or whether this period of inactivity is forced upon them by their environment. Several times it has been stated that a few fertilised eggs have hatched shortly after they were laid. POWERS and TANNREUTHER have observed, in different species of *Asplanchna*, that occasionally a female that is producing the normal fertilized eggs enveloped in a thick inner shell, produces an egg which lacks this thick inner envelope. Such eggs hatch soon after being laid. This would seem to indicate that the thick shell may in some manner determine the time of hatching of the eggs. SHULL has found that a few resting eggs of *Hydatina senta* hatch soon after being laid. Whether their shells were normal or abnormal was not determined.

LITE and WHITNEY show, with regard to *Brachionus Bakeri*, that young rotifers are unable to break through the egg membranes because of the firmness of the new membrane. If newly laid fertilised eggs of *Brachionus* and *Asplanchna* are kept for a few days in sealed containers amid a mass of decomposing organic material, the covering membranes of the eggs are weakened, and the young rotifers can readily break through them. Such eggs develop and hatch slowly or quickly according to the amount of aeration in the culture water. The thick inner membrane of the resting eggs of *Asplanchna* causes the development of the young rotifers to cease probably because it shuts off the oxygen supply. Abnormally fertilised eggs which lack this thick membrane may produce the young females that may hatch inside the body of the mother as do the parthenogenetic eggs or, if laid, hatch soon afterwards. In this way it should be possible to understand that *Asplanchna* females are able to produce both male young, female young, and fertilised eggs; a fact which would otherwise be contradictory to the theories of sex-determination.

LEHMENSICK (1926 p. 37) has studied the life conditions and ripening of the egg of *Euchlanis triquetra* and *Asplanchna priodonta*. The development of the embryo of an amictic female (*Euchlanis triquetra*) lasts 34—36 hours. The first egg is laid on the third or fourth day, two eggs are produced a day. The animal lives 2—4 days after the last egg has been laid. The number of amictic eggs produced is 24; the number of male eggs is the same, but they are laid in a much shorter time and the mictic female lives for about 4—6 days after the last egg has been laid. The

mictic females always occur at the height of the culture after fecundation, they are always recognisable by the dark vitellarium, caused by deposition of fat substances. The production of resting eggs strongly influences the ovarium; the development takes much more time, and their number is but small. This is also the case with *Brachionus urceolaris* (SACHSE 1912); *Hydatina* (PLATE 1886; LENSSEN 1888; STORCH 1924 and MARINELLI 1925). Pairing after the first day has no influence.

In *Asplanchna priodonta*, *Euchlanis triquetra* and *Synchaeta pectinata* LEHMENSICK finds the same differences between mictic and amictic ovaries as found by STORCH in *Hydatina*. He has very thoroughly studied the manner in which the yolk masses are transferred to the amictic egg.

A. O. TAUSON began her very important investigations relating to the sex determining influences upon *Asplanchna intermedia* in 1925. The main results of her paper (1925 p. 131) are as follows. *A. intermedia* may even at an older age be impregnated; the age is of no significance in this respect: (against MAUPAS, PUNNET, WHITNEY o. a. and in accordance with the observations of LAUTERBORN and ZAWADOWSKY); the mictic females produce 9—10 (smaller) eggs; the amictic ones 5—6 (larger), the first-named lives only three days; it is ripe upon the first day; produces about 10—12 eggs upon the second; continues egg production on the third whereupon it dies; an amictic female lives 5—6 days; produces only about 4 eggs a day. A female may both produce larger and smaller females; variations in the external medium influence the ovarium, most probably causing variation in the amount of yolk mass, again causing production of smaller eggs, resulting in the smaller females which produce the mictic females. Fertilised mictic females grow strongly in size, reaching that of the amictic ones; the yolk mass is altered in aspect, and the shell of the eggs is another. The development of the resting eggs does not require desiccation, but very low temperatures near or below zero. The resting period begins after the development has begun, most probably at a stage of about 10 blastomeres. In Nature the course for *A. intermedia* is as follows: The resting egg is hatched in May; the propagation is only parthenogenetic; the water is filled with amictic females. This stage lasts a week, then the amictic females begin to produce simultaneously mictic and amictic females: the first produce males, never resting eggs; again a period with only amictic females occurs; again there appears a period with mictic as well as amictic females, and now the mictic displace the amictic ones; the males live for a very short time, fecundate the mictic ones; they produce two or three resting eggs, whereupon they die. The whole active period lasts only about a month. On the locality *A. i.* mainly feeds on *Anuræa*; when these disappear and the water-bloom period begins, *A. intermedia* disappears. The main results with regard to the sex determining influences of external conditions are as follows.

It is the medium reaction and the quantity of carbonates in the physico-chemical variations in the external medium which may be regarded as one of the

main factors causing the occurrence of the mictic females. The reaction is not direct but makes its influence felt in accordance with its strength ("durch den Grad ihrer Veränderung" TAUSON p. 320). The direction is indifferent. With regard to the carbonates the percentage maximum of the mictic females is reduced by augmentation and augmented by reduction. The influence of these two factors is obvious in all generations of *Asplanchna intermedia*. The general amount of salts has not the same influence as carbonates; the same is the case with the other components of the amount of salts in fresh water. On the other hand, they influence the growth and the beginning of the ripening of the sexual products; the other substances dissolved in fresh water (organic substances, free carbon dioxide and oxygen) have no influence at all upon sex determination. —

In a second paper (1926 p. 355) TAUSON emphasises her view that it is the physico-chemical variations in the external medium which cause the development of mictic females. Especially the variations in pH and their influence are thoroughly studied.

It has been shown that *A. intermedia* does not endure an acid reduction below pH 6.70. TAUSON shows that pH, during a day and night period, especially during a water-bloom period, is subject to very significant oscillations from 6,8 to 9 or even more; these variations belong only to the surface layers, not to the deeper water layers, where the pH reaction is rather constant. TAUSON now shows experimentally that variations in pH caused by a supply of NaOH, if they are only of short duration, have no influence upon the production of mictic females. Only a constant long-lasting influence on the part of the reaction variation in the external medium is able to influence the production of mictic females.

In this way it is intelligible that the day and night variations in pH do not cause the appearance of a sexual period; if life conditions in the superior water-layers do not suit the animals, they have only to wander downwards into deeper ones.

TAUSON furthermore shows that the temperature optimum for *A. intermedia* lies at 16—23° C.; at a temperature of 10—11° C. the life of the species is threatened; at 10 the propagation is stopped, but the specimens live 7—9 days without showing signs of senility. Optimum is at 17° C.; at 20—22° the energy of the specimen is exhausted much faster and the lifetime abbreviated. 25° C. and higher temperatures have a fatal effect.

In accordance with the publications of JATZENKO on *Anuræa aculeata* and *Synchaeta pectinata* TAUSON supposes that the upper limit for plancton rotifers lies at 25° C., the lower for *Anuræa aculeata* and *Synchaeta pectinata* at 4°. Besides, TAUSON states the result from almost all earlier authors that the differences in temperature do not influence the appearance of mictic females. — The same is the case with the Ca-ion; on the other hand, "bei den pH Aenderung nach der alkalischen Seite wirkt Ca lähmend auf die Entwicklung und den Wuchs der Tiere; bei der saurer



Reaktion dagegen tritt das Ca-Ion als Antagonist des Cl-Ions auf" (p. 389). The life conditions of the animals are ameliorated.

In a very convincing manner TAUSON (p. 387) has shown how the periodicity of *A. intermedia* in the natural ponds is in full accordance with the annual variations in the physico-chemical conditions of the pond-water in which the animals live.

The resting eggs are not hatched if pH is below 6.89—6.90 and if the temperature is below 13.5—14. Optimum is at pH 7.11—7.15 and a temperature of 17° C.; at that time only amictic females appear. If the temperature is lowered the *Asplanchna* max. is detained, even if pH is 6.90—7.00; when it again reaches 17—18, the amictic propagation sets in again, and when the high temperatures 22—23° C. appear, and pH reaches 7.7—8.00 (waterbloom), the mictic females appear. The *Asplanchna* accommodate themselves to the new life conditions, amictic propagation takes place again, but the appearance of high temperatures 24—25° C. and a fall in pH to 7 cause mictic females to appear again; the bad life conditions now cause the number of mictic females to be uninterruptedly augmented; the large amount of males, now produced, fecundate the mictic females which produce resting eggs and the period of active life of the colony is at an end. —

In the paper (1927 p. 343) TAUSON examines whether oxygen may have any sex determining influence on the Rotifera. As mentioned above, SHULL has maintained this, whereas WHITNEY has denied it. TAUSON arrives at the same result as SHULL and LADOFF, maintaining "dass der Sauerstoff nur im Falle der Uebersättigung ein wirksamer die Geschlechtbestimmung beeinflussender Faktor ist". She criticises WHITNEY and shows why he has arrived at a result differing from SHULL's and her own.

Then TAUSON (p. 353) maintains that neither quantitative nor qualitative variation in nourishment has any great sex determining influence upon the Rotifera; the former has almost always been denied, the latter has been maintained by WHITNEY (1917) and others, as well as by LUNTZ (1926). She asserts that the results of the experimental work of LUNTZ (see later) have not been interpreted in the right way, and that it is the variation in the reaction of the medium which is sex determining. For when a culture of protozoa is conveyed to a faintly acid medium, the Protozoa will alcalise the culture water, and it is this factor which acts to determine the sex. With regard to variations in the quantitative amount of food, TAUSON maintains that these variations are not without all sex determining influence. Amictic females which have had no food for three days and are then given copious nourishment, produce mictic ones in the following days.

Finally TAUSON (p. 357) recapitulates all her investigations in the following main results.

The most active sex determining factor is the variation in the reaction of the water, then decreasing amount of food, and lastly and in smaller degree the amount

of oxygen and carbonates; all other factors, also the temperature, only play an indirect rôle. —

The most important factor in the external medium is the reaction acting in the first place with regard to its strength, however, only to a certain limit; if the pH value is augmented above 0.60, under natural conditions the amount of mictic females are not augmented; the reaction is felt in all generations, from the first, developed from the resting egg, to the last. —

The second sex determining factor is an insufficient amount of nutriment, causing smaller eggs, giving rise to mictic females, again producing males. These alone cannot hold the place for the species, and the active life of the colony is brought to an end. Renewed better life conditions may cause the amictic females to begin amictic propagation again, a new maximum may set in, later on followed by a new sexual period.

The third sex determining factor is the oxygen acting only "bei der Veränderung seines Gehalts in der Richtung der Vergrößerung des Sättigungsgrades des Wassers mit Sauerstoff".

The fourth and last sex determining factor is the amount of carbonates; directly they do not cause the production of mictic females; if their amount is augmented they have a repressing influence upon the maximal development of mictic females.

Variations in temperature have no sex determining influence, but between the limits 16°—23° C. they augment the influence of the reaction.

LUNTZ (1926 p. 233) has studied the factors determining sex in *Pterodina elliptica*. The investigation was based upon "reine Linien" i. e. parthenogenetic progeny from one single animal. With constant external conditions (temperature, nourishment) only five young were born; this number was quite constant, and under these conditions males never appeared; during 93 generations all were amictic females.

The main result of LUNTZ' investigations is that *Pterodina elliptica*, under constant external conditions, propagates only parthenogenetically (93 amictic generations without variation in size and with the normal remarkably small number of eggs). On the other hand, if life-conditions are altered, quite distinct variations in the external medium are able to force the production of mictic females, but the limits for the appearance of mictic females are much more restricted than those which limit life in the active stage for the amictic ones. In this way LUNTZ has shown that these variations are of the greatest significance for sex determination.

The investigations show that owing to qualitative but not quantitative variation in food (*Polytoma-Chlamydomonas*) amictic females can be forced to produce as well mictic as amictic females; on the other hand, mictic females cannot be forced to produce amictic ones, while between the two sorts of females there are profound physiological differences. Differences in temperature alone cannot force amictic females to produce mictic ones, but combined with variation in food they can cause the augmentation in number of the mictic females.

The hydrogen ion concentration has no direct influence as a sex determining factor; on the other hand, it makes its influence felt because for every concentration it has very sharp limits between which variation in nourishment is only able to produce mictic females. To variation in concentration only the descendants of the last (the fifth) egg react in parthenogenetic cultures; to variation in food the descendants from all eggs react simultaneously; the property of the fifth egg is not hereditary because, if selection has been carried out in five generations, the reaction to the concentration is again normal.

Males and resting eggs only appear in colonies with two females; in this case a mother cannot be fertilised by a son.

The relative age of the mother has no influence with regard to the production of mictic females.

Under quite special conditions resting eggs are developed after 6—10 days; from resting eggs amictic females are always produced, but these females may, under special conditions, be forced to produce mictic females.

With regard to the question if an internal rhythmic hereditary factor has a similar significance, LUNTZ denies this, maintaining that the alteration of generations is only dependent upon variations in external conditions. The results of the outdoor explorations (LAUTERBORN, W.-L.), and GOLDSMIDT'S deductions mainly supported by SHULL'S explorations, are interpreted in another way. —

In a second paper (1929 p. 193) LUNTZ arrives at a somewhat different result. For he saw that, even if the rotifers were kept under certain constant life conditions, males and resting eggs appeared in the cultures, and that at quite regular intervals of the sexual periods. For further investigations he now used *Brachionus Bakeri* var. *rheanus*. The lifetime was twelve days; number of eggs 7; in this species, in contradistinction to *Pterodina elliptica*, the mictic female could be paired with its own sons; it only produces a single resting egg. It was of course of interest to see if variations in external conditions could influence the periods between two sexual periods, either shortening or prolonging them. LUNTZ has shown that a mixed nourishment of *Eudorina* and *Chlamydomonas* in reality influenced the period so as to prolong it.

If resting eggs are transferred to 0.086 p. c. nutrient solution or to a strong acid or alkaline solution, it is possible to force already the first generation to produce mictic females. Further investigations with *Pterodina elliptica* showed that here, too, mictic females and males appeared at regular intervals, and that even if the animals were kept under quite homogeneous life conditions. The main result of the paper seems to be that constant life conditions are not able to prevent periods in which mictic females appear, and so to speak appear quite spontaneously and at regular intervals. LUNTZ further shows (p. 206) that variation in food with regard to *Brachionus* and acid nutrient solution in *Pterodina* is able to produce periodic periods of bisexuality, and that other constant variations in life conditions are able to prevent the appearance of mictic females. From these last named observations LUNTZ is of opinion that in spite of the fact that mictic females in cultures, under homogeneous life conditions, so to

speak appear in waves at regular intervals, the observations nevertheless clearly show that it is only variations in external conditions which condition the appearance of mictic females. I shall return to this main point later on.

FINESINGER (1926 p. 63) has tried to test the direct effects of various chemical and physical agents on the egg-productivity and length of life in a parthenogenetic rotifer *Lecane inermis* (Bryce) and to determine whether any of the effects produced are heritable.

*Lecane inermis* seems to reproduce purely parthenogenetically, thus assuring a pure line. Its average length of life is about eight days, during which it lays about fifteen eggs. The eggs hatch in eighteen to twenty-four hours, and the young begin to produce eggs in twenty-four to thirty-six hours after hatching. The maximum size is reached on the fourth or fifth day. The main result was that the subjection of *Lecane* to varied chemical environments and to higher temperatures for a period of three months through about twenty-five generations has been ineffective in transmitting diversities beyond the second generation, and the effects of subjection to varied temperatures were transmitted for two generations (two weeks) after return to normal, then disappeared.

WATZKA (1928 p. 430) in a series of experiments tried to elucidate the factors supposed to cause the appearance of males in *Asplanchna Brightwelli*, *Brachionus pala* and *Anuræa aculeata*. Like almost all other investigators, he arrives at the result that temperature alone has no influence; the same is the case with starvation and variation in light; also want of oxygen had no influence; only sudden variation in nourishment caused an increase of males of 60 %, and already on the fourth or fifth day after the variation had set in.

JENNINGS and LYNCH (1928 p. 347) have begun a study relating to length of life and fertility in the rotifer *Proales sordida* Gosse. Quite correctly the authors maintain that these two features, life and fertility, are characteristics in the same sense as are colour of eyes or form of body, revealing in the same way the influence of genetic and other factors. JENNINGS and his pupils' investigations with regard to the Protozoa indicate that the situation in this group appears to realize very closely the conditions demanded by the neo-Larmarckian theory: slow and steady changes under pressure of environment; the changes produced being cumulative and passed on to progeny even under altered environments; until finally these altered environments produce anew another set of changes. In the Metazoa there is thus far little experimental evidence of such racial alteration under the influence of the environment; the authors have therefore preferred to acquire personally experimental knowledge of these matters, and used for their studies the above-named *Proales sordida*. Length of life and fertility directly affect survival and elimination; stocks or individuals having greater length of life and higher fertility, through that very fact tend to prevail over and replace stocks having those characteristics in a less degree. The usual length of life of the animal is about eight days. The number of eggs produced is normally twenty-four to twenty-eight. The offspring

of young parents show a lower fecundity than the offspring of the same parents when old. Late-born individuals show much greater diversities in fecundity among selves than the early-born, and late-born individuals have on the average a longer embryonic period of immaturity, and a longer interval from the egg of one generation to the first egg of the next. The cause of this differences is that the eggs produced by young parents are small and very uniform in size. Older and larger parents lay larger eggs: of the latest eggs many of the largest and the smallest fail to develop. Now it has been shown that the peculiarities of the individuals are correlated with the differences in size of eggs; that is with the different amount of cytoplasm and yolk that they contain. In sum, the individuals of a clone of *Proales sordida* are not all intrinsically alike. They are diverse in fecundity and in the length of certain of the life periods: in dependence on the size of the eggs from which they come, and, through the latter, in dependence on the age of their parents.

In the next paper (II) JENNINGS and LYNCH have taken up the details of the life-history, particularly in so far as they throw light on diversities in length of life and fecundity. The main results are the following. Four periods are distinguishable: the embryonic and immature periods, lasting each about one day; the period of fecundity, lasting three to nine days, and the period of old age lasting up to eighteen days. The mortality in these various periods differs very much. In eggs from old parents there is a high mortality in the embryonic period, in the eggs from young parents a low mortality or none; in the period of immaturity there is practically no mortality; it increases with the beginning of egg laying. The production of eggs is a severe process. Individuals that successfully survive the period of reproduction may live for a period of old age that is two to three times as long as the total earlier life.

WHITNEY (1929 p. 416) has studied the chromosome cycle in the rotifer *Asplanchna amphora*. WHITNEY here tried to determine whether there is any apparent relation between chromosomes and the production of male- and female-producing daughters. Earlier investigations have shown that daughters of a parthenogenetic mother who receive a scanty diet of green *Chlamydomonas* will be amictic, whereas daughters of a parthenogenetic mother receiving an abundance of *Chlamydomonas* will be mictic; furthermore that excess of oxygen will give rise to a higher percentage of male-producing daughters than would be the case in culture waters having the amount of oxygen that is normally absorbed from the atmosphere.

Furthermore TAUSON has ascertained that a sudden change in hydrogen-ion concentration in the water will also bring about a higher production of mictic females. Finally SHULL found that the mechanism which determines the nature of the daughters was in operation in the mother, at the time her eggs, which later developed into her daughters, were forming their single polocyte. Now WHITNEY states that the diploid number of twenty-six chromosomes was found in the mature parthenogenetic female-producing eggs, and also in the somatic cells of the female embryos

developing from such eggs. In the maturation stages of a few of these eggs the chromosomes were markedly larger than in the corresponding stages of the majority of the eggs. On the other hand, whether this difference in the size of the chromosome is correlated with male and female-producing individuals could not be determined. The mature parthenogenetic male-producing eggs contain the haploid number of thirteen chromosomes, a number which was found also in the somatic cells of the young male embryos. The mature sexual eggs contain thirteen chromosomes. Two sorts of spermatozoa occur, viz. mobile spermatozoa containing thirteen chromosomes, and non-mobile and rudimentary spermatozoa deriving from spermatids containing fewer than thirteen chromosomes. The mobile spermatozoa unite with the parthenogenetic male-producing eggs; both contain thirteen chromosomes, thus producing the fertilised eggs with the diploid number of twenty-six chromosomes. These fertilised eggs develop into female-producing ones which produce parthenogenetically.

With regard to the number of polar bodies in the Rotifera the records differ very much. Apart from earlier papers, the questions relating to the number of chromosomes, the reduction of the chromosomes and the whole process of the maturation of the rotifer eggs have mainly been dealt with by ERLANGER and LAUTERBORN (*Asplanchna* 1897) LENSSEN (*Hydatina* 1898) WHITNEY (*Hydatina* 1908 b) SHULL (*Hydatina* 1910) and TAUSON (*Asplanchna* 1924). The main results of the investigation are that the male parthenogenetic egg casts out two polar bodies, the female parthenogenetic egg casts out only one polar body; the resting eggs behave like the male parthenogenetic eggs, producing two polar bodies.

With regard to cytology STORCH has shown that there are conspicuous differences in the ovaria of the two females.

The mictic eggs, the male eggs, as well as the resting eggs, derive from the same origin. Already in the youngest ovocyte stage a synaptic prophase is performed; a pseudo-reduction of chromosomes takes place, a diakinesis is developed and finally normal "Reife-Teilungen" go on. The haploid number of chromosomes is eight. If this kind of egg is not fecundated, a male with haploid chromosome number is the result. If it is fecundated, the result is a resting egg, with diploid chromosome number; from this egg a female is developed. On the other hand, the nuclei of the ovocyte of the amictic females are typical "Ruhekerne", resting nuclei, and therefore in a condition quite atypical of nuclei in sexual cells; they have an atypic prophase and only pass through one meiosis, and the egg remains diploid. In this way it approaches the soma cell. The mictic egg passes through all stages from diploid through haploid and again to diploid; in the amictic one this whole nucleo-metamorphosis is obliterated. WHITNEY (1929) arrives at quite similar results.

NACHTWEY has shown with regard to *Asplanchna amphora* that the staining power of the nuclei of the ovocyte of the amictic females is very small; this is due to an emersion of chromatin substance; the nucleus itself is colourless, but

the substance which is able to be stained, is deposited externally and later on fused into "Kernkappen".

On the other hand, it seems that in the nuclei of the ovocytes in some of the embryos the greater part of the chromatin remains within the nucleus, and hence "Kernkappen" are not developed. It is presumed that mictic females will develop from these embryos. —

If now we survey what has been gained mainly by the laboratory studies relating to the biology of the Rotifera, and especially with regard to sex determination, we shall arrive at the following results.

1. As males have never been found in *Bdelloida*, it has been supposed that this group only propagates parthenogenetically. It has been presumed (DOBERS 1915) that desiccation and contraction as a process of renovation play a similar rôle to fecundation in the biology of the animals. It must, however, be kept in mind that thorough experimental investigations have never been carried out. — Experimental studies relating to some *Notommatidae: Proales*, and to *Lecane* seem to show that parthenogenetic propagation is at all events the rule and perhaps exclusively so also in families outside the *Bdelloida*. (NOYES, BIANCO, FINESINGER).

2. The propagation of the *Seisonacea*, seems to be exclusively bisexual; more thorough investigations are desirable.

3. Among all other Rotifera heterogeneous propagation is, as far as we know, the rule.

4. All heterogonetic Rotifera possess two sorts of females, the amictic and the mictic ones; the amictic females always propagate parthenogenetically and only produce females, the egg has only one polar body, fecundation has no influence.

5. The mictic females may also propagate parthenogenetically but then only produce males; they may be fecundated whereupon they produce resting eggs; resting eggs are merely fecundated male eggs. The spermatozoon suppresses the male qualifications of the resting egg and causes female development; the egg has two polar bodies; the two sorts of females are strictly separated and cannot pass over into each other.

6. From the resting egg a female is always developed, fecundation therefore determines the sex in two generations, first in that developed from the male egg, and secondly in that developed from the resting egg.

7. The female hatched from the resting egg is always amictic, but already the next generation may consist of mictic and amictic females. LUNTZ (1929) shows that if resting eggs (*Brachionus Bakeri*) are transferred to 0.086 % acid or alkaline solutions, it is possible to force the first generation to produce mictic females.

8. It has been maintained that fecundation is only of importance if it takes place in the first hours of the life of the young females, later on it has no influence. (MAUPAS, PUNNETT, WHITNEY, MITCHELL). On the other hand LAUTERBORN, ZAWADOWSKY, TAUSON, and LUNTZ maintain that also older females can be fecundated; in this respect the species seem to differ from each other.

9. The life of the male is extremely short, never more than a few days, most probably often only a few hours; it may be ready for fecundation the very moment in which it is born (*Diglena volvocicola* ZAWADOWSKI 1916). The same may be the case with the female (*A. Ebbesbornii* TANNREUTHER 1920) but commonly the female lives some days before fecundation. Even if some observations seem to show (LUNTZ: *Pterodina elliptica*) that a son cannot fecundate the mother animal, this is not the rule for the rotifers. As stated by TANNREUTHER (1920), in viviparous species a male may fecundate the mother animal before it is born; the pairing process as a rule takes place not through the oviduct but through the hypodermis; the spermatozoa are found swimming freely in the body cavity and force their way to the eggs in the ovarium, whereupon fecundation takes place.

10. Mictic females may successively lay first male eggs and then resting-eggs or simultaneously carry resting-eggs and male embryos. This has been observed in *Asplanchna* species (LAUTERBORN 1893; v. ERLANGER u. LAUTERBORN 1897; LAUTERBORN 1898; LANGE 1913; LEHMENSICK 1926) in *Notommata Werneckii* (BALBIANI 1878); in *Pedalion mirum* (LAUTERBORN 1898); in *Hydatina* (NUSSBAUM 1897 and SHULL 1910). Females which produce both eggs from which amictic females are developed and male eggs have not been observed. The few exceptions from this common rule may all be interpreted in another way.

In viviparous species the same female may produce larger and smaller females; from the first are developed females which only produce females of the type of the mother animal; from the last-named male producers, mictic females (TAUSON 1926).

11. It has been shown (WHITNEY 1912, SHULL 1911 o. a.) that lines obtained from widely separated localities yield a constantly differing proportion of mictic females and behave very differently with regard to the number of eggs, etc.

12. Parthenogenetic propagation carried on for a very long time causes a weakening of the colony which can be neutralized by mictic propagation (WHITNEY 1912).

13. At high temperatures mictic females lay more eggs than amictic ones.

14. The experimental investigations have greatly contributed to our knowledge of lifetime, fecundity and period of embryonic life.

The best studied species are *Hydatina senta* (PLATE 1886; MAUPAS 1890; NUSSBAUM 1893; WHITNEY 1907—1929; SHULL 1907—1929).

1912. SACHSE *Brachionus species*.

1922. NOYES *Proales decipiens*.

1928. JENNINGS and LYNCH *Proales sordida*.



1926. LEHMENSICK *Euchlanis triquetra*.  
 1916. ZAWADOWSKY *Diglena volvocicola*.  
 1926. FINESINGER *Lecane inermis*.  
 1926. TAUSON *Asplanchna intermedia*.  
 1926. LUNTZ *Pterodina elliptica*.  
 1929. LUNTZ *Brachionus Bakeri*.  
 1925. CORI *Apsilus vorax*.

All these investigations show 1) that the lifetime of the different species is a rather constant factor 2) that it is very different in the different species.

Very short-lived are species such as *Proales decipiens*, *P. sordida* and *Lecane inermis* (5 to 8 days); the lifetime of *Hydatina senta* and *Euchlanis triquetra* is about 2—3 weeks; of the *Brachionus* species one to two weeks; of the benthonic species somewhat longer. *Apsilus vorax* lives remarkably long, about 6 weeks (CORI); the lifetime of the *Asplanchna* species may be put at about 2—3 weeks. With regard to the *Bdelloida*, ZELINKA (1891) SPEMANN (1924) and DOBERS (1915) have shown that the lifetime of some species is much longer: of *Callidina lutea* and *roseola* e. g. five months (ZELINKA); of antarctic *Bdelloida* several years, the active period of life being only several months, but these months being distributed over years, interrupted by long periods in an aphytic condition (MURRAY 1910).

15. Also the fecundity of the species differs very much but is rather constant for the single species. It is very small for *Pterodina elliptica*, which lay only 5 eggs. Most of the species investigated lay about 20—30 eggs; *Hydatina senta* lay remarkably many eggs, about 50. The viviparous species get relatively few young ones, rarely more than 10, and commonly a smaller number (*Rotifer vulgaris*, the *Asplanchna* species). All these statements apply to the amictic females. The number of eggs a mictic female produces depends on whether or not she is fertilised. If not fertilised, investigations hitherto carried out seem to show that the number of eggs laid by the two sorts of females is almost the same, but that those of the mictic female are laid in a much shorter time (LEHMENSICK 1920: *Euchlanis*). If fertilised, the production of resting eggs is an exertion on the part of the whole organism, of course influencing especially the vitellarium; this latter becomes darker, the yolk spherules become larger and more abundant. (TANNREUTHER 1920 a. o. TAUSON 1927).

16. It has formerly been supposed that a female only lays one resting egg and recently STORCH (1924) and MARINELLI (1925) have supposed the same. This may be correct for species which die with the resting egg in the body, but it is not the rule. The *Brachionus* species produce a varying number. (*B. urceolaris* 5—6 SACHSE 1912); *Euchlanis triquetra* several (LEHMENSICK 1926); *Hydatina senta* about 10; *Asplanchna Ebbesbornii* 1—8 (TANNREUTHER 1926). It has been shown that in some species (*Asplanchna Ebbesbornii*) there exist two sorts of resting eggs (TANNREUTHER 1920) thin shelled and thick shelled ones; only the last-named are real resting

eggs from a biological point of view; both kinds of eggs have two polar bodies. As generally known, a period of inactivity seems to be necessary for the normal development of the resting-eggs. That this, however, is not always the case has been observed several times (SHULL: *Hydatina senta* a. o.). Through LITE and WHITNEY'S investigations (1925) it has been observed (*Brachionus Bakeri*) that young Rotifera are unable to break through the thick egg shells but that these shells, when the eggs have been kept in decomposing organic material, are weakened, and that the young slip out when the eggs are kept in well aerated water; it seems probable that it is the exclusion of oxygen which causes the retardation in the development of resting eggs.

17. There are no external differences between the two kinds of females, it has been maintained (v. ERLANGER, LAUTERBORN *Asplanchna priodonta*, LANGE A. *Ebbesbornii* 1912), that the mictic females are smaller than the amictic ones. The truth may be that they are born smaller (*Asplanchna*, *Synchæta*) but that later on they reach the size of the amictic ones.

Even if we know, especially through STORCH'S and NACHTWEY'S investigations, that there are cytological differences between the mictic and the amictic females, we are of course unable in this way to distinguish the two kinds of females from each other in the living stage. This will, however, always be possible in those species where the females carry their eggs, the three kinds of eggs showing great differences with regard to size and shell structure. It is furthermore often possible where the females do not carry the eggs. As often stated by experimenters, the vitellarium gets a darker colour owing to fat production, and owing to this fact it is often very obvious when the mictic females in a colony have appeared.

18. It is often maintained that the mictic females appear at the height of development of a colony; the significance of this observation will be more thoroughly dealt with later on.

19. In reality it seems as if the question of sex determination in the Rotifera is solved. It is fecundation which determines if an egg shall develop into a male or into a female. A resting egg is only the fecundated male egg and a male egg is a resting egg which is not fecundated; the spermatozoon introduced alters the sex of the egg. What has not hitherto been sufficiently elucidated is what those factors are which determine that amictic females shall continue with the production of amictic progeny or begin to produce mictic progeny. In reality this has no direct bearing on questions relating to sex determination; it bears only on those factors which determine the appearance of another kind of females. This has not always been understood, but has been strongly emphasized by recent authors (e. g. SHULL). — In reality sex is determined a generation in advance and all investigators should therefore concentrate their attention not upon the mothers but upon the grandmothers (SHULL 1913, ZAWADOWSKY 1916). The mechanism which determines the nature of the daughters was in operation in the mother at the time when her eggs, which later developed into her daughters, were forming their single polocyst; in

reality all investigations, especially those of recent years, have been directed precisely towards that point.

20. As mentioned above, TAUSON (1926 a, b) has shown with regard to *A. intermedia* that an amictic female may produce large as well as small females. Variations of different kind influence the ovarium, most probably causing variation in the amount of yolk-mass, which again causes production of larger or smaller eggs resulting in larger and smaller amictic females. Already a series of earlier authors have pointed out the differences in the structure of the ovary in the mictic and the amictic female.

What then are the factors which, according to experimental studies, cause a colony of amictic females to begin producing mictic females and in this way inaugurating a sexual period.

21. The external conditions which have been supposed to bring about the production of mictic females are temperature, nutrition and chemical substances.

Light which seems to influence the cycle of aphids has, as far as we know, no influence upon the cycle of rotifers (WATZKA 1928).

Temperature does not seem to have any direct influence upon the cycle of Rotifera. It has been maintained by MAUPAS (1891) and SHULL (1911 a), but while MAUPAS got an augmentation of the number of mictic females at high temperatures, SHULL got the same at low ones. MAUPAS supposed that the influence was a direct one; SHULL that it was indirect. Most authors have been unable to find any influence at all (PUNNET 1906, WHITNEY 1907, NOYES 1922, WATZKA 1928). An indirect influence is most probably unquestionable. High temperatures cause phenomena of depression, which again cause the appearance of mictic females; furthermore the influence of the variations of pH is dependent upon the variations of temperature (TAUSON 1926 a; 1927 b).

Nutrition. The investigations seem to show that the influence of the nutrition is much greater than that of the temperature. Some authors (PUNNETT 1906) and WHITNEY, during his first investigations 1907, of recent years ZAWADOVSKY 1916; LUNTZ 1926; NOYES 1922) find no influence. NUSSBAUM (1897) maintains a direct influence, finding that starvation causes the production of mictic females. On the other hand, a series of authors (MITCHELL 1913 a, b); WHITNEY in a series of papers after 1907 (1916 a, 1917 a and 1919) arrive at the result that a high state of nutrition promotes the production of mictic females. That nutrition is a cycle-altering factor is also maintained by SHULL (1917 a and 1917 b and by TAUSON 1927 b) but only in the way that the amount of food alters the chemical composition of the water, or combined with variations in pH, which is maintained to be the main factor. —

Especially from the investigations of WHITNEY (1914 a, b, 1916 a, b) it was shown that change of food causes production of mictic females. WHITNEY changed

the food from green *Chlamydomonas* to colourless *Polytoma* and obtained a great increase in the number of mictic females. He first regarded the result as directly caused by the new food; later on he thought that it was the direct change which had this effect; this was corroborated by all the following authors (HODGKINSON 1918; LUNTZ 1926 and WATZKA 1928). Whenever the food was changed from *Chlamydomonas* to *Polytoma*, or from *Polytoma* to *Chlamydomonas*, the result was the same. LUNTZ deepens the question, pointing out that, if change of food is to produce the appearance of mictic females, two successive generations before must be given a single kind of food, furthermore, that the effect of change of food is dependent also upon the pH value.

Chemical substances. It was SHULL (1910, 1911 a) who first of all showed that the chemical composition of the water could influence the cycle of rotifers. If *Hydatina* was kept in a strong solution of horse manure, mictic females disappeared. Later on SHULL (1911) further showed that of the components of the manure it was in the first place urea and ammonium salts which caused the mictic females to disappear. The same was the case with a long series of other substances (1913 a). How these components caused this result was not clear.

As a result of investigations begun already in (1910) and carried on later by TAUSON (1925, 1926 a, b, 1927 b) and by LUNTZ (1926) it was pointed out that mictic females were produced precisely if the medium was changed into a very dilute fresh manure solution. Hence, in this case, too, it seems that it is not the new factor introduced, which causes the appearance of mictic females, but it is the change itself from one medium to another which is the primus motor.

As mentioned above, WHITNEY had shown that mictic females could be produced by the introduction of *Chlamydomonas* in the cultures. As this phenomenon could presumably be traced to an increase in the amount of oxygen in the medium, SHULL and LADOFF (1916) tried to find out whether oxygen itself could be regarded as a factor causing the appearance of mictic females. This really seemed to be the case to some extent, but fresh investigations by WHITNEY (1917 and 1919) and WATZKA (1928) did not seem to support these views. During recent years inquirers have tried to find out whether pH had any influence upon the production of mictic females. The results are rather curious. TAUSON (1925) maintains, with regard to *A. intermedia*, that the pH value of all factors is the most effective in causing the appearance of mictic females in both directions. With regard to *Pterodina elliptica* LUNTZ (1926) can find no influence at all — it is only influenced through change of food.

TAUSON (1925) showed that increase of carbonate diminishes the production of mictic females, the other substances have no influence.

Any one who has studied the whole literature relating to sex-determination in rotifers, will again and again find the word change. He will receive the impression that more than the introduced factor itself, it is the change from the

old to the new one, which may have the sex determining influence. It is the change of food in both directions from *Chlamydomonas* to *Polytoma* and from *Polytoma* to *Chlamydomonas*, from low pH values to high values or vice versa, from one chemical composition of the medium to another, which causes the appearance of mictic females. On the other hand, the change may by no means always be responsible for the appearance of mictic females. In many cases change has had no influence. We may now consider yet another important sex-determining factor which has not been mentioned hitherto, and which is nearly related to the internal factors.

22. The influence of all the above-named external factors, temperature, nourishment, chemical composition, light etc. is not the same at all periods of the life of the animal. Labile periods may occur as well as periods in which all external factors have no influence at all. With regard to the Rotifera SHULL (1912) has shown that the decision whether the egg shall give rise to a mictic or to an amictic female, is in reality made in the three first hours before the egg is laid, i. e. during the maturation process. Later on external factors have no influence. — All investigations seem to corroborate this supposition.

23. We will now turn to the internal sex-determining factors. SHULL (1910) (*Hydatina*) showed that mictic females were commonest in the middle of their mother families, not so common at the beginning and at the end. On the other hand, this sentence was not always corroborated; not by LUNTZ (1926) for *Pterodina elliptica*, nor for *Asplanchna intermedia* (TAUSON 1927 b). It has often been maintained that, in the Rotifera, as was supposed by WEISMANN with regard to the Cladocera, we have an inherent cycle, in which the occurrence of mictic females is bound to distinct generations which mostly appear independently of variations in external conditions. From studies in Nature with regard to the periodicity of Rotifera, LAUTERBORN arrived at this result in 1898. DIEFFENBACH and SACHSE (1912) came to a similar result. Laboratory students commonly arrived at another result. Only PUNNETT (1906) arrived at the same result as LAUTERBORN and DIEFFENBACH and SACHSE. But little by little, the more elaborate the laboratory investigations were made, the more the inquirers were forced to admit that even if life conditions were quite unaltered, males could occur rather suddenly and in waves at regular intervals (WHITNEY 1912 a, SHULL 1915 b, LUNTZ 1929). The phenomenon is connected with the fact that in aquaria it may happen that species appear and disappear at quite regular intervals, periods begin with amictic females and finish with resting-eggs laid by mictic females; between two consecutive periods of life in active stages there may elapse e. g. two months (*Asplanchna ebbesbornii*, TANNREUTHER 1920 p. 389). The phenomenon is most probably indisputable but is interpreted in very different ways. SHULL maintains that the periodicity is internal, and sees in heredity one of the most important factors in the determination of sex (1923). MITCHELL (1913 a, b) maintains that the periodicity is dependent upon changes in nutrition, a

result disputed by SHULL (1915 b) who supposes that qualitative differences probably do not influence the interval between periods of many males.

The observation that, under quite homogeneous life conditions, males in cultures appear in waves at conspicuous intervals, LUNTZ (1929) would interpret as due to an external factor only; nothing shows that in the said Rotifera we have anything to do with an internal factor "Das einzige was vererbt wird ist die Fähigkeit auf bestimmte äussere Reize durch Erzeugung von Männchen zu reagieren, wobei diese Reaktion auch eine zyklische Form annehmen kann. Dadurch wird aber die ganze Vorstellung von einem vererbten Rhythmus hinfällig . . . . . der Rhythmus kommt nur als Reaktion auf äussere Reize zustande. . . . . Allem Anschein nach handelt es sich hier um eine Summierung von bestimmten (vielleicht schädlichen?) Einflüssen". This may be correct. On the other hand, I cannot see better than that the dispute is now reduced to a mere dispute of words. A "Summierung von bestimmten Einflüssen" is, as far as I can see, only another expression for inherited characters and as such belongs to the category of internal conditions.

Continued investigations have furthermore shown that even if male waves set in suddenly, they may in some cases decrease gradually. (WHITNEY 1912 a, SHULL 1912). SHULL (1912 and later on, 1923) explained the phenomenon as a result of long continued undisturbed metabolism, caused by long continued parthenogenesis.

The observation that males and mictic females in the colonies under laboratory conditions appear in waves, is nearly related to the result of outdoor explorations, that their appearance in Nature is periodic.

24. Of course the question has often been raised: In what manner can external conditions influence the organism?

An examination of the Kernplasma-relation by SHULL (1922 a) showed that in the Rotifera this seems to have no influence upon the cycle of reproduction.

STORCK (1923 and 1924) found highly refractive bodies outside the nuclear membrane of the oocytes of the mictic, but not of the amictic females. Whether these bodies have anything to do with the change of the egg from amictic to mictic, and whether we could perhaps in this way see the result of the influence of external conditions is an unsolved question.

WHITNEY (1929) has tried to determine whether there is any relation between chromosomes and the production of mictic and amictic females. It has been shown that both eggs possess the diploid number of twenty-six chromosomes, but that in a few of these eggs the chromosomes were markedly larger than in the corresponding stages of the majority of the eggs. On the other hand, correlated relations with mictic and amictic females could not be pointed out.

TAUSON (1926 a, b) seems to come nearest to an explanation. As stated above, she observed that an amictic mother at a certain moment gives rise to smaller as well as to larger eggs (the former developing into mictic, the latter into amictic females), and that the production of these two different sizes of eggs depends upon variations in

the yolk-mass which are again dependent upon variations in the external medium. If these observations are of general import, we may here probably have the way in which external conditions force their way to the ovary of the amictic female and in this way make their influence upon the periodicity felt.

Beyond these facts I cannot see that these investigations have contributed to the understanding of how the cycle is altered by variations in the external medium. —

### b. The Seasonal Variations.

It is a well-known fact that some of the Rotifera, especially the plancton Rotifera belonging to the old group "*Loricata*", are subject to very great variability. This is especially the case with species belonging to the Genera *Anurea*, *Notholca*, *Schizocerca* and *Brachionus*, but also with some "*Illoricata*": *Polyarthra*, *Triarthra*, *Asplanchna*; with the perennial species much more than with the pronounced summer forms (*Anuraopsis hypelasma* a. o.). The phenomenon originally caused the creation of a lot of species, of the genus *Anurea*, thus more than 30; they are now reduced to only two main forms, *A. aculeata* Ehrenberg and *A. cochlearis* Gosse; we find quite the same phenomena with regard to Plancton-Crustacea, Plancton-Flagellata and Plancton-diatoms. —

With regard to the reduction of the Rotifera this took place from c. 1895 to about 1900, the principal authors being WEBER (1898) ROUSSELET (1897). The so-called buoyancy theory (OSTWALD and WESENBERG-LUND) was an attempt to elucidate the facts; it was especially based upon the study of the Plancton Cladocera. As a working theory it has presumably not been without significance; WOLTERECK (1913) has tried to weaken its importance. As far as I can see, the investigations of WOLTERECK have served much more to deepen the importance of the theory, than to make it superfluous. In this respect I refer the reader to the papers of WESENBERG-LUND (1926), ROBERT (1928) and LUNTZ (1929). During the period in which the great reduction in the number of species took place it was intelligible that several authors went further than was quite correct. There is no doubt that my conception of the *Synchæta-species* (W.-L. 1898) corrected by ROUSSELET (1897) and LAUTERBORN (1903 p. 596) was wrong; the same is the case with v. DADAY (1903 p. 599) who supposed, that *A. aculeata* and *cochlearis* belonged to the same species.

In the seasonal variations or cyclomorphoses LAUTERBORN saw accommodations to variations in the external medium: "lückenlose Formenreihen deren einzelne Glieder in Abhängigkeit von bestimmten äusseren in ihrer Gesamtheit erkennbaren, . . . . . Bedingungen im Kreislaufe des Jahres gesetzmässig aufeinander folgen (1900 p. 612)". LAUTERBORN relies on his excellent studies on the seasonal variations of *Anurea cochlearis*. He arrived at the main result that in some ponds, especially old

ones rich in vegetation, "treten mit Beginn der wärmeren Jahreszeit nebeneinander die *Tecta-Hispida-Irregularis*-Reihen auf, deren Endglieder typische Sommerformen darstellen". . . . Ponds which are of a new date, artificial ponds and with a central part free from vegetation "fehlen diese Variationsreihen so gut wie völlig; sie werden durch die var. *robusta* ersetzt".

Later authors and among them also myself have to some extent corroborated LAUTERBORN'S statements; very many ponds are found in which the variation-series *tecta*, *hispida* and *irregularis* have not been developed; the forms *hispida* and *irregularis*, where present, are, as LAUTERBORN maintains, typical summer forms. The same cannot be said with regard to the form *tecta*. Later investigations have shown, however, that these cyclomorphoses are of a much more complicated nature than LAUTERBORN as well as myself originally thought.

In a very instructive paper KRÄTZSCHMAR (1908, p. 1), with regard to *Anuræa aculeata*, arrived at results very different from those of LAUTERBORN with regard to *A. cochlearis*.

Firstly KRÄTZSCHMAR shows that in the Lunzer lakes forma *brevispina* was common from June to August 1907, whereas it was almost lacking in June—August 1906. KRÄTZSCHMAR is unable to find the regularity in the cyclomorphoses and periodicity of *A. aculeata* which characterises LAUTERBORN'S *A. cochlearis*. Here he is in accordance with earlier authors (VOIGT (1904), HUBER (1905), LOZERON (1902), WALDVOGEL 1900) and it may now be added with very many recent authors. Only upon one single point is he able to find regularity: The resting-eggs appear in June and July, and the forms which sooner or later develop from them are always longispine forms. He furthermore adds the new very significant fact: that the resting-eggs are always carried by *brevispine* forms. Later on KRÄTZSCHMAR tried to solve the question relating to the cyclomorphosis experimentally.

He is right when he says that cyclomorphosis such as he has got to know it, has nothing to do with a morphological construction, because the single stages in the series of variations derive in the series of generations from the very same mother animal, not, as was the case with LAUTERBORN'S series, from different mothers and from different waters. He shows, firstly, that none of the variations in the surrounding medium, neither temperature, nor viscosity, nor light, nor any amount of nourishment, are able to influence the form of the *Anuræa aculeata*; what they are able to do is only to accelerate or retard the development.

KRÄTZSCHMAR therefore comes to the result that the life of the species *Anuræa* during a year is governed by two parallel cyclus phenomena, viz. the sexual cyclus and a morphological one, a reduction series, ("Formenkreis"). When these two cycles simultaneously reach their minima, as is the rule in Nature, the species arrives at a stage when it needs to return to the point from which the cycle started; a sexual period is the result; resting-eggs are formed, and when these are hatched, large *longispine* forms appear again. The cyclomorphosis is a process of senility, a slowly augmenting decline in the vitality of the females which propagate



exclusively parthenogenetically. According to KRÄTZSCHMAR the seasonal variations are governed by internal and not by external conditions.

That KRÄTZSCHMAR's studies have in many respects brought the question nearer to its solution is beyond all doubt. On the other hand, like all who have worked with these difficult problems, he has generalized too much. He has not been aware that the *Anuræas* disappear not only for months but also for years from the plancton of a pond and then suddenly appear again, most probably hatched from resting-eggs lying over for months and years; his criticism of LAUTERBORN is justifiable, but he seems (1908) to be unaware of the fact that the plancton-*Anuræa* from the largest lakes show no seasonal variation, and often seem to be acyclic; at all events sexual periods are very rarely observed. In other words: the cyclomorphoses are but slightly developed just where they should be expected i. e. where the sexual periods are wanting: in larger lakes).

LANGE (1911, p. 38 and 1913, p. 441) has been able to corroborate several of KRÄTZSCHMAR's results. He showed that 200 resting-eggs laid by *Asplanchna Sieboldi*, when hatched, gave *A. Brightwelli*. i. e. that the sacklike processes characteristic of *A. Sieboldi* (= *A. Ebbesbornii* Hudson) are not developed in the first generation deriving from the resting-egg; he further showed that they do not appear until the third or fourth generation. POWERS (1912 p. 454) arrived at quite the same result with regard to *Asplanchna amphora*. I shall return to this point later on.

DIEFFENBACH (1912 p. 21) saw with regard to *Anuræa aculeata* that robust forms with long posterior thorns were hatched from resting-eggs, and SACHSE (1912 p. 76) ascertained that *Brachionus pala* (no posterior thorns) were hatched from resting-eggs, whereas the forms with posterior thorns (*B. amphiceros*) did not appear until later, during parthenogenetic development.

In accordance with all these authors LANGE, together with KRÄTZSCHMAR and LAUTERBORN, concludes that the phylogenetic oldest form is the result of the bisexual propagation, and that the parthenogenetic period is to be regarded as the labile period during which factors of different kind may exert their influence.

What is gained here must be regarded as very valuable established facts which, as far as I can see, HARTMANN's investigations mentioned later on are not able to weaken.

The great question is, however, of what nature these factors are which cause the seasonal variations in the Rotifera during the parthenogenetic periods.

LAUTERBORN (1900, p. 611) was inclined to accept my old standpoint (1900, p. 617) corrected by OSTWALD (1902) and to seek the origin of the variations of the Rotifera in the regular physical variations of the fresh water. From very short series of observations and from observations relating to a very modest reduction of posterior thorns caused by insufficient nourishment, DIEFFENBACH (1912) very categorically and in accordance with his mentor WOLTERECK arrives at the peremptorily expressed result that "einzig und allein die schwankende Ernährung" is responsible for the seasonal variations. This assertion is disputed by de BEAU-

CHAMP (1928, p. 91) and, as far as I know, by almost all other inquirers. Only KRÄTZSCHMAR has thought it necessary, owing to DIEFFENBACH's very insufficient investigations, to weaken his own clear and thorough investigations in a second paper (1913 p. 44). He would now divide *Anuræa aculeata* (1913 p. 49) into two subspecies of which one is supposed to be able to vary in accordance with variations in the amount of nourishment (*Anuræa aculeata variabilis*) the other, *A. aculeata s. str.* Ehrenberg, not. The first is said to belong to the small ponds, the second to larger ponds and lakes. That this is an easy way of smoothing out the divergences between two authors cannot be denied; but this proceeding, if it were commonly adopted, would be fatal to all scientific work; that the two presumed subspecies should be distinguishable from each other by the structure of the shell of the resting-egg is of very little value. In different species e. g. in the *Asplanchna*, *Synchaeta*, *Brachionus* the thickness and structure of this shell is subject to very great individual variations; it may partly be determined by external conditions, partly by internal ones (the number in the series of eggs produced). To see a specific character in this structure is unquestionably a very dangerous matter. —

In a rather extensive paper HARTMANN (1918 p. 209) has given a series of observations relating to the polymorphism of the Rotifera. As far as I can see, the material upon which the explanation is based is rather small and the deductions very wide-ranging. The main results are most probably as follows: HARTMANN confirms the result of earlier authors that series of reduction (Reduktionsserien) do really occur. He further maintains that the animals deriving from the resting-eggs, are not always longispine, but may belong to specimens with posterior thorns of middle length, and that series of addition as well as series of reduction may occur; the series of addition should be a result of better nourishment and higher temperatures. This may be true, but as far as I can see, the material warrants neither the many deductions nor an attack on the views of earlier inquirers.

*Anuræa aculeata* is assumed to be divided into two species *A. aculeata* and *A. valga*; the last-named species is said to be hatched from a resting-egg, and later on slowly to acquire the missing thorn through a series of additions. It may, however, be pointed out that, as far as I can see, hitherto no *Anuræa valga* has ever been hatched from a resting-egg, just as an *A. tecta* has never been hatched from the resting-egg of *A. cochlearis*.

During the years 1900—1925 an almost incredible number of papers dealing with fresh-water plancton have appeared. Almost all the samples upon which the investigations were based contained rotifers, commonly relatively few species; in the lakes in the first place *Anuræa* species, in the ponds species of *Anuræa Brachionus*, furthermore *Asplanchna*, *Synchaeta*, *Triarthra* and *Polyarthra*. The buoyancy theory, well known as it was, was in some degree a testimony that the author was up to date with regard to his general scientific equipment, and the result was that the thorns of the *Anuræa* and *Brachionus* were again and again studied in the light of the buoyancy theory. In the dawn of the theory many of the investigations

gave results which seemed to corroborate the theory; later on, when variations in nutriment were made responsible for the variations, most of the investigators came to the opposite result. It would take very long to clear up these very different results, scattered, I believe, in several hundred papers, and very often occupying only a few pages or lines in each. There is no reason for doing so, inasmuch as DE BEAUCHAMP (1928 p. 86—100) has already done a good deal towards it.

I confess that in regard to this literature paternity cannot in the first place be combined with fatherly pride. I may perhaps be allowed to remark that the buoyancy theory was primarily based upon studies relating to seasonal variations in some of the plancton Cladocera; these seasonal variations have been rather thoroughly studied, and the main results of these studies have always been corroborated. With regard to all the other plancton organisms, it was only shown that many of these, too, such as Flagellata, Diatoms, Rotifera were subject to great variations, and that at all events some of these variations were seasonal variations, running parallel to those of the plancton Cladocera. It would seem that all authors have supposed that the polymorphism of the plancton Rotifera could be used as a weapon against the buoyancy theory. They have had no clear idea of the fact that in the Cladocera and the Rotifera, (Arthropods and Vermes) external conditions have had a very different material to act upon. That the great annual, physical and chemical variations in fresh water could set their stamp upon the first-named so as to bring about regular seasonal variations, whereas this could only rarely be the case with the Rotifera I will try to elucidate in the last part of this treatise. I will further show that if they are able to do so, they must necessarily manifest themselves in quite another way. Here I only wish to lay stress on one single point.

Whatever the many planctologists have found, whether or not they hold that the variations of the Rotifera are in accordance with the buoyancy theory, they have all furnished their quota to it. All have pointed out that the perennial Rotifera are subject to a very conspicuous variation, differing from lake to lake and from pond to pond, the same main result which characterizes the principal forms of the plancton Cladocera, Flagellata and Diatoms. Furthermore they have shown that the pronounced summer-forms, which only live at the highest temperatures, *Ploesoma*, *Gastropus* and some *Rattulidæ*, show nothing of all this; furthermore that pronounced polymorphism is a phenomenon which only seems to belong to the plancton Rotifera, not to the benthonic species.

From de BEAUCHAMP'S and my own investigations it now seems warranted to suppose that the Rotifera were originally benthonic creeping organisms, which have slowly taken possession of the free water-masses; the vegetation in ponds and smaller lakes may, *sit venia verbo*, be regarded as the springboard from which the type has pushed off and reached the pelagic region. Different lines of development from benthonic to pelagic species have been traced. The last-named all seem to be regarded as the final stages in long developmental series, leading from the

benthonic into the pelagic region. The rotifers living here have in greater or less degree obtained the so-called planctonic characters, characterizing the inhabitants of this part of the water-areas, whether belonging to the sea or to fresh water. As examples may be mentioned: great hyalinity, means of augmenting the cross-section resistance, means to counteract the inconvenience of living in a medium without supporting planes (perceptible especially with regard to material whereupon the eggs may be fixed). Among these characters we must also mention for fresh water organisms, a great power of variation, a pronounced ability to bring about accordance between the structure of the organism and the regular annual variations in life conditions in the free water-masses of fresh water; a variation which shows itself locally as well as temporally. There can be no doubt that form-variation has reached a much higher development among pelagic than among benthonic fresh water organisms, and may be regarded as a pronounced plancton character like hyalinity, structures counteracting the falling velocity etc. Now it is very interesting to see that the Rotifera are governed by the same law. The more the Rotifera pass from benthonic to pelagic life, the more they become perennial plancton organisms, the higher is the variability, locally as well as temporally. This is the main result of all plancton investigations. And it was only this main result which would be required by the buoyancy theory if it were right. On the other hand, to demand that the regular annual variations in the external medium should manifest themselves in quite the same manner in two parts of the animal kingdom, differing so much from each other as the Crustacea and Vermes really do, is in my opinion no sign of high scientific training in those who claim this. The question now is, why this variation does not manifest itself so conspicuously and so regularly as in the Cladocera. We will return to this point later on.

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## Chapter II.

### Some Remarks relating to the Ponds used for the Investigation.

The material investigated has mainly been gathered in Nature and studied in the living state in the laboratory immediately after the samples had been taken; the life history of *Hydatina*, *Asplanchna* species and some other species was simultaneously studied in cultures in the laboratory. In 1898 an investigation was carried out in eleven small ponds, situated in the north-eastern part of Seeland, six in the neighbourhood of Hillerød, 5 near the little village of Holte about twenty kilometres south of Hillerød. — Samples were taken every fortnight, and the material as far as possible determined in the living state. Simultaneously samples were preserved in formaline. The results of the investigation have in part been published in my

Plancton Investigations Vol. I. The investigation was mainly carried out to support the plancton investigations in the lakes; I refer the reader to my Plancton Investigations (1904, p. 13). —

In the year 1922—1925 regular investigations were again carried out in seven ponds. These ponds were 1) Frederiksborg Castle Lake, 2) the Island Pond (Ødam) 3) the Funke Pond, 4) the Horseshoe Pond, 5) Nøddebo Pond, all lying near Hillerød, and furthermore, 6) Fredensborg Pond and 7) Asminderød Pond, lying near Fredensborg, 9 kilometres north of Hillerød; of these ponds Nos. 1 and 2 are the same which were regularly explored in 1898. During the period 1898—1926 regular explorations have been carried out in different ponds, and smaller lakes e. g. Gripsø, Løgsø, Agersø and ponds near Hellebæk.

The samples in these ponds were taken either every week or every fortnight, but mainly only during the summer months; the first sample was taken shortly after the thawing of the pond, the last when the temperature in November dropped to about 6—8° C. At that time rotifer life in all the ponds was almost the same. —

Apart from these more regular explorations during the period 1900—1926, excursions were carried out every year very often during the summer months, now to one now to another pond; this was mainly the case where ponds were found which either contained rare Rotifera or where some species seemed to show either peculiar sexual phenomena or remarkable seasonal variations. In this way, during the last 30 years, numerous samples have been examined from several hundred ponds and smaller lakes, most of them lying in North Seeland, some of them near my summer laboratory near Tjustrup lake in the middle of Seeland. These ponds were not visited at regular intervals all the year round, but most of them were explored many times, and at almost all seasons of the year.

The net used was Müller gauze No. 25; now and then gauze No. 12 was also used, especially for the larger species (*Asplanchna*) and the Crustacea. One sample was preserved in formaline on the spot, the other, was brought living to the laboratory and examined immediately. In the course of an hour most of the rotifers had gathered in the lighted border of the vessel; from here a sample was taken with a pipette and the rotifers anæsthetised in Beauchamp's fluid and later on killed with Flemming's fluid, whereupon the samples were preserved in formaline. From all the samples slides were made, partly from the plancton from the pond, partly only of the rotifer sample deriving from the lighted border of the vessel. The samples were preserved in formaline and encircled with Rützw's sealing-wax. Most of the samples dating from 1922 are still very good and have been consulted during the writing of this treatise. —

During the last few years motor-cars have been used; most of the samples have been taken by myself, the last few years by my assistants, especially Mr. KAI BERG to whom I tender my most cordial thanks for his help. —

To give a special description of any of these ponds is probably unnecessary. With regard to the above-named smaller ponds and lakes I shall restrict myself to

the following remarks. All may be supposed to be natural waters, a few are perhaps dug out, but if so, more than a hundred years ago; since then they have been undisturbed. — The largest is Frederiksborg Castle Lake, 22 ha with a maximum depth of a little more than 3 m. Gribsø is about 14 ha with a maximum depth of 13 m. Løgsø is about 12 ha and has a maximum, depth of about 7 m., all the other ponds are much smaller, the largest, Funkedam and Ødam (the Island Pond) only about 2 ha and some of them as Nøddebo Pond, Fredensborg Pond, Asminderød Pond, have only a circumference of a few hundred meters. None of them dry out during the summer and only Nøddebo Pond will most probably freeze to the bottom in severe winters. The maximum depth of Funkedam is about 2 m., all the other ponds are about  $\frac{1}{2}$ —1 m. deep.

It is a common feature of all these lakelets and ponds that from the time when the ice has disappeared and till the first part of June they have surfaces quite free from vegetation. The Castle Lake, Horseshoe Pond, Fredensborg Pond and Asminderød Pond are quite free from vegetation the whole year round; of higher plants the Castle Lake contains hardly any but *Polygonum amphibium*, *Myriophyllum* and *Potamogeton crispus*, none of them play any significant role in the lake. From June to late autumn the surface of the Island Pond is covered with a carpet of *Nymphaea alba* and *Nuphar luteum* leaves, spotted with those of *Hydrocharis morsus ranæ*. A good deal of the surface has no vegetation. In 1890 the Funke Pond was almost free from vegetation. During the period 1890 to 1928 the vegetation beginning at the eastern part of the pond slowly covered  $\frac{3}{4}$  of the whole surface. The principal plants are *Potamogeton natans*, in the bays *Stratiotes aloides*, *Myriophyllum* and *Ceratophyllum*. From the last part of July to November these plants fill the water with an enormous amount of leaves and stalks, every autumn leaving a thick layer of undecayed material at the bottom. Nøddebo Pond, Asminderød Pond and Fredensborg Pond may in the main be designated as village ponds extremely rich in organic matter; the last-named pond has during the last year become so polluted from a sewer, that the water is coloured gray; the pollution is augmented from year to year and has now reached such a degree, that the originally very interesting rotifer-plancton has been almost totally altered into a combined Infusoria and *Actinurus* plancton.

In 1920—23 Nøddebo Pond was almost changed into a moist meadow and was then again dug out in 1924; the depth was then  $\frac{1}{2}$  m. During 1924—26 it was quite free from vegetation, but from 1926 an overfilling with thread algæ, especially *Spirogyra*, began, so that the water may now, especially after June, be regarded almost as a thick mass of algæ, without any free water-mass. Suddenly in 1927 *Elodea* appeared; now in 1929 the pond is packed with it.

With regard to the Funke Pond the investigation covers a very long series of observations. — This has been carried out for special purposes. — It is quite obvious that the surface of a pond, during the process of being grown over, is slowly covered with floating leaves, and that the water-layers will be filled with

stems and leaves. Invariably the result will be that the central part of the pond, originally free from vegetation and forming a veritable pelagic region, will be lost during the process. Simultaneously the organisms belonging to the free water-masses of the pond are almost always forced to disappear, leaving room for the society of organisms belonging to ponds filled with vegetation. As far as I know, we do not find any description in the literature of how the plancton in the history of a smaller lake or pond alters its character. Funke Pond has been extremely well-known to me ever since my childhood. In 1880 its whole surface was almost totally free from vegetation; only a narrow girdle of *Potamogeton natans* was found in the eastern part of the pond. It was in the same pond that I began my plancton studies. During 1890—1900 it had a rich plancton of diatoms, especially *Asterionella gracillima*, and every year from 1890 to this very day, the pond has been visited many times a year, and in several years at all events every fortnight. Till 1890 *Potamogeton lucens* predominated in the eastern part of the lake, but during the period 1890—1900 *P. natans* slowly conquered the surface, and *P. lucens* was superseded; it still lives in a few specimens in the eastern part of the lake. Almost simultaneously a few *Nuphar luteum* appeared in the central parts of the pond; hitherto the plant was only found near the *Typha angustifolium*, *Sparganium ramosum* and *Scirpus lacuster* vegetation bordering the pond.

For some years these *Nuphar* plants only grew very slowly, but in 1910 they had formed a belt across the pond, which in this way was divided into an eastern and a western part during the summer months. During 1910—1920 the eastern part was now packed with *Myriophyllum* and *Ceratophyllum*, and from the northern side the *Typha* and *Sparganium* vegetation grew southward out into the pond. The whole summer the surface of the eastern part was covered with an extremely luxuriant carpet of *P. natans* and of *Hydrocharis morsus ranæ*; from 1920 *Stratiotes aloides* became an inmate of the pond; a little earlier *Nymphaea alba*.

Most probably long before the observations were begun, a great part of the bottom was covered with a thick blackish-green carpet of *Fontinalis*, which plays a considerable rôle in all our smaller ponds. From 1920 in July—September a blue-green alga, covered the whole vegetation with a thick blue-green layer.

The thick vegetation in the eastern part has deposited such a great amount of decaying matter that the bottom of the pond has been raised very much. No bottom fauna has been able to destroy all this material; it has not been submitted to any coprogenous process and here, as almost everywhere in ponds of this nature, the bottom is covered with a brown coarse-grained substance, in Sweden and Denmark commonly designated as Dy. Most probably in the course of some few decades the vegetation from the shore of the pond will conquer the whole eastern part and alter it into swamp and at last into a meadow. The pond follows the rule common to all our fresh-waters; as long as the shore vegetation, the *Scirpus-Phragmites* zone, or, as here, the *Typha-Sparganium* zone, is the main vegetable factor which causes the elevation of the bottom, this process goes on extremely slowly. On the other

hand, as soon as the surface has been conquered by plants with floating leaves, in Denmark especially *P. natans* and the *Nymphæaceæ*, the elevation takes place with extreme rapidity; the sedimented material is not changed into coprogenous matter; it acquires a different character and this again influences the colour, the chemical composition of the water, and the temperature.

Now during the period 1925—1929 the depth of the pond in the eastern part was only about  $\frac{3}{4}$  m.; the bottom material is Dy; it is almost lifeless and covered with *Fontinalis* overgrown with a blue-green alga; in the western part there is still a now rather small "pelagic region" the depth here is  $1\frac{1}{2}$  m.; *Chironomidæ*, *Oligochaeta* and *Pisidium* are still to be found, and the coprogenous processes are still going on; the bottom material may in the main be designated as Gytje. —

The variations in the plancton have been followed since 1900. At that time the plancton was characterized by large maxima of diatoms, especially *Asterionella gracillima*, *Fragilaria crotonensis* and *Synedra acus* var. *delicatissima*, but already in 1910 *Fragilaria crotonensis* disappeared; curiously enough a few specimens were found in May 1923. *Synedra acus* has not been found after 1914. *Asterionella* had very large spring maxima in 1900—1910 and was again common in autumn; during this period it was among the principal forms of the pond; later on it steadily diminished in quantity. After a severe ice-winter, during which the pond was icebound for more than 100 days, the plancton diatoms seem practically to have disappeared; but every year *Asterionella* appears in the spring but in rather small quantity. In 1900 and most probably for a very long time before that, the Flagellata have played the most prominent part in the plancton during the summer months. During spring *Dinobryum sertularia* and *Peridinium* had very large maxima; in company with them *Synura uvella*, *Uroglena volvox* and species of the genus *Mallomonas* were found. During summer, at the highest temperature, *Ceratium hirundinella* had enormous maxima; in May as well in August the water was coloured yellowish brown, in May mainly by *Dinobryum*, in August almost only by *Ceratium*. Sometimes, in July—August, the colour was caused by *Mallomonas*. No particular differences could be pointed out before 1920; then it was as if the maxima were smaller, but suddenly after the severe winter in 1924 it seems as if most of the Flagellata which before that time had predominated, were now much rarer. This holds good especially for *Ceratium hirundinella*; the commonest now are *Synura uvella* and *Uroglena volvox*, but after 1924 one thing seems quite certain, we have never observed the water to be coloured by Flagellata; it has the brown clear colour well known from so many of our smaller ponds. Whether the great Flagellata maxima will appear again only the future can decide. —

Cyanophyceæ have hardly ever been found in the pond plancton, and the Chlorophyceæ have always played a very inconspicuous rôle; the principal forms being *Eudorina elegans*, *Pediastrum* species and *Botryococcus Braunii*. —

With regard to the Cladocera it may be pointed out that no *Daphnia* and no *Ceriodaphnia* have been found in the pelagic region. Furthermore it is very interest-



ing that *Daphnella brachyura* has been found during the summer months from 1900 to 1913; it has always been rare, but since 1913 not a single individual has been seen. — The main form of Cladocera represented has always been *Bosmina longirostris*, often with enormous maxima appearing at different times during the summer months. After 1920, however, the maxima became smaller and smaller, and in the year 1927—28 they were very small. Simultaneously with this we may substantiate another very peculiar fact. During the last four years a series of Cladocera belonging to the vegetation zone have been found in ever increasing number in the “pelagic region”. This holds good especially for *Chydorus sphaericus*, *Acroperus harpæ*, *Graptoleberis testudinaria*, *Scapholeberis mucronata*, *Anchistrocerus oviventris*, *Alona* sp. *Pleuroxus* sp. This shows that organisms belonging to the vegetation take possession of the central parts of the pond even before the vegetation itself has conquered it. The main forms of the Copepoda are *Diaptomus gracilis*, which has always been rare, and *Cyclops strenuus*. It may further be added that in 1928—29 I more than once saw *Æschna* larvæ as well as *Acilius sulcatus* as imago cross the pond.

Now, proceeding to the Rotifera, it may be pointed out that the fauna in the pelagic region originally, in 1900—1910, was rich and interesting. Curiously enough the *Brachionus* species have always been rare. *B. pala* has never been observed, and of the others *B. angularis* has only been observed a single time. *Anuræa aculeata* has only rarely had large maxima. The main forms have been *Anuræa cochlearis*, *Polyarthra platyptera*, *Synchæta tremula* and *S. pectinata*. These four species have commonly formed the greater part of the rotifer plancton, and until 1924 their conspicuous and often large maxima have been followed by sexual periods. Of the *Asplanchna* species, *A. priodonta* is almost always present, but generally in small number. Several times, and especially during July—August, it has had enormous maxima, colouring the water milky, and, then, in bright sunshine, standing  $\frac{3}{4}$  M. from the surface.

Until 1910 *Ascomorpha agilis* was a pronounced spring form laying its eggs on the *Asterionella* colonies. Especially characteristic of the rotifer plancton of the lake was the fact that the “pelagic region” until 1910 possessed a very conspicuous fauna of summer rotifers, namely *Gastropus stylifer*, *Pedalion mirum*, *Pompholyx sulcata*, *Anuræa hypelasma*, *Rattulus hamatus*.

After 1910 this fauna became rarer and rarer, and in 1923 all these forms had disappeared or were only present in very small number. It seems as if the rotifer fauna of the pond now consists almost only of *Anuræa cochlearis*, *Polyarthra platyptera*, a little *Asplanchna priodonta*, *Synchæta tremula* and *S. pectinata*; all the other species are only present in a very limited number. But also with regard to the Rotifera do we see the peculiar phenomenon that species belonging to the vegetation zone slowly conquer the region. This is especially the case with species such as *Sacculus viridis*, *Euchlanis dilatata* and *Euchlanis triquetra*, *Dinocharis pocillum*, and *Notommata* sp.

## Chapter III.

A comparison between the Danish Lake Plancton and  
Pond Plancton.

For several years I have studied the periodicity of the pond plancton in many localities. This was especially the case in the above-named pond exploration in 1898 and later on in the same 7 ponds in 1922—24, in which I studied the rotifer plancton. From all these ponds lists tabulating periodicity, and the temperature of the air and water have been made. Especially because I know that these lists are very insufficient, and that many organisms have been determined with doubt and most probably incorrectly, they will never be published. They are presumably of some scientific value, no less than so many other lists of the phytoplankton printed in plancton papers and relating to the periodicity of Baltic ponds and smaller lakes. In my eyes all these lists are, however, of very slight scientific value. In 1928 Mr. GUNNAR NYGAARD at my request began an investigation of the phytoplankton, especially the nannoplankton of Frederiksborg Castle Lake. Whereas my lists only contained about 15 phytoplanktons, NYGAARD owing to better methods and after a year's regular explorations has found 74 species in the same lake (1929 p. 266). Mr. NYGAARD has now on the same principles begun a regular investigation of the nannoplankton in 14 ponds near Hillerød, some of them the very same which have been subject to regular investigation with regard to Rotifera (W.-L.) or Crustacea (W.-L. and BERG). Already now I am quite sure that even if planctologists may master the Zooplankton, only algologists can subject the Phytoplankton and especially the Nannoplankton, which cannot be separated from the Phytoplankton, to a valuable scientific treatment. The treatment hitherto given to the nannoplankton on the part of planctologists, has been very casual; therefore all conclusions with regard to the nannoplankton in fresh water as a source of nutriment for the other plancton organisms are of a very problematic nature.

These periodic investigations of the pond plancton which, apart from those on the Rotifera, have taken much of my time, have given the following main results.

1. Our pond plancton differs very much in composition from the lake plancton. Whereas the diatoms have large maxima in all our lakes, they are almost absent in the ponds. The *Melosira* may still occur in larger ponds such as Frederiksborg Castle Lake, in smaller ones I have hitherto only rarely found them; *Fragilaria crotonensis*, *Synedra acus* and *Rhizosolenia* have only been observed rather rarely; of all diatoms *Asterionella gracillima* seems to be the form which has best adapted itself to live in rather small ponds; it may occur even in ponds with rather large Cyanophyce maxima, but has then its maximum before that of the Cyanophyce; the *Cyclotella* species play a greater rôle than I had hitherto supposed. — The Flagellata maxima are commonly much larger in ponds than in lakes. We may indeed find the *Dinobryum* species, *Uroglena volvox*, *Synura uvella* and *Peridinium*

species in lakes, but of these species only the *Dinobryum* attains large maxima here. In ponds the Flagellata-maxima may be so large that the water often gets a yellowish colour; often the plancton-net, when drawn only for a moment, is covered on its inner side with a slimy coat; this applies especially to *Dinobryum*, whose huge maxima may occur at almost all seasons of the year, perhaps with the exception of November—February. Only *Ceratium hirundinella* is really a pronounced lakeform, whose maxima in lakes may, as is generally known, be enormous. It may also have large maxima in rather small ponds, but here it may often be displaced by *Ceratium cornutum*. — MALLOMONAS with the main species *M. acaroides* may occur in lakes, but the large maxima have only been observed in ponds. When our ponds so often, especially in June, have a yellowish colour, it is almost always due to one of the above-named Flagellata. If the colour is predominant in the last part of July and in August, it is almost always caused by *Ceratium hirundinella*; in a few ponds *Euglena sanguineum* colours the water red in bright sunshine; in cloudy weather green. This is caused by the fact that, in bright sunshine, the Euglena lie as a scum upon the surface, whereas, in cloudy weather, they are more homogeneously distributed in the water-layers, the Chlorophyceae and yellowish brown Flagellata being then able to give the water this colour.

The main part of the Cyanophyceae belongs to ponds or the water areas termed pond lakes. True plancton organisms in larger lakes, forming large maxima there, are few, mainly species belonging to the genera *Lyngbya* and *Oscillatoria*; of the other *Coelosphaerium Kützingianum*, *Anabaena flos aquae* are some of the forms most frequently to be found in rather large lakes. The waterbloom phenomenon so characteristic of our pond lakes and ponds, is rare in those of our freshwaters which may be termed lakes; where it occurs, it is mainly due to material produced in shallower water areas, pond lakes, from which it is carried out into the lake with the outflow. This is the case e. g. with the enormous maxima of *Aphanizomenon flos aquae*, which are produced in Salten Langsø and from it through Gudenaå poured out into the other Silkeborg lakes. *Gloiostrichia echinulata* is only known from a very few smaller lakes.

Unquestionably the pelagic region of our largest lakes contains many species of Chlorophyceae; some of them are mentioned in my Plancton Investigations, but more thorough explorations are wanting. It is, however, mainly in the ponds that a large number of hitherto very little known Chlorophyceae may occur. The Desmidiaceae have their high maxima especially in ponds with high pH values; many of the *Volvocales* especially *Chlamydomonadales*, mainly in highly eutrophic ponds. Most of these forms only rarely form maxima which colour the water; ponds which are coloured green are by no means so numerous in Denmark as those which are coloured either yellowish by Flagellata or bluegreen by Cyanophyceae. Huge maxima in ponds are mainly produced by *Volvox*, *Eudorina elegans* and, in very small ponds by *Pandorina morum*. In some ponds upon the heaths of Jutland I have found some *Coelastrum* species (*C. pulcrum* presumably plays a very great rôle). In village

ponds *Botryococcus Braunii* may now and then attain enormous maxima, causing a peculiar, very beautiful, brilliant green colour. A few of our ponds near Hillerød e. g. the Island Pond (Ødam), has a beautiful emerald colour in summer, caused by *Volvox*.

One year Frederiksborg Castle Lake showed a similar colour caused by *V. globator*. The pelagic flora of our Chlorophyceae, especially that of the ponds, stands in great need of investigation.

Whereas the Protozoa only play a very inconspicuous role in the pelagic region of our lakes, they are much more prominent in the ponds. Peculiar to the lake plancton are mainly *Staurophrya elegans*, *Tintinnidium fluviatile*, *Codonella lacustris* and some *Heliozoa*; in the ponds *Dileptus trachelioides*, *Bursaria truncatella*, *Prorodon ovum*, *Epistylis lacustris*, *Didinium nasutum*, *Coleps hirtus* are very common.

With regard to the Rotifera it may be pointed out that in my area of exploration I have been unable to find a single species which is strictly bound to the lake plancton. All Rotifera from the pelagic region of our largest lakes may also be found in rather small ponds; on the other hand, specimens from the lakes have often a special stamp, owing to which they were formerly regarded as new species or are still designated as varieties (*Asplanchna priodonta* var. *helvetica*, *Triarthra longisetula* var. *limnetica*; etc). All in all the community of Rotifera from the central parts of ponds have a rather different aspect to that from the pelagic region of the lakes. Here the Rotifera almost always play a rather inconspicuous rôle, whereas in ponds they have very large maxima and often of the same species as in the lakes. The principal forms in the lakes: *Triarthra longisetula*, *Anuræa aculeata*, and *A. cochlearis*, *Polyarthra platyptera* and *Asplanchna priodonta* are also the principal forms in the ponds; the pronounced summer-forms, such as *Ploesoma Hudsoni*, *Gastropus stylifer*, *Rattulus hamatus*, *Anapus testudo*, may all have large maxima in our ponds and especially in our pond-lakes. Apart from all these forms, the ponds, however, contain a rather large series of Rotifera. As all these species will be mentioned in the following part of this work I shall not enter into detail here but only point out that the *Brachionus* species play a dominant rôle in the central part of the ponds, whereas they are very inconspicuous in the lake plancton. The main forms are *B. angularis* and *B. pala*. This result is in accordance with that of other scientists. —

Apart from the Rotifera named in the following list which are characteristic of the central part of the ponds, a long series of Rotifera is to be found which belongs mainly to the vegetation, but during the sexual period, and especially in ponds which are about to lose a "pelagic region", get a semi-pelagic stage in their life and live in the central part of the ponds. These species will be mentioned in the following. The list of the Rotifera normally found in the central part of ponds and in lakes comprises 51 species.

- Notommata* sp.  
 — sp.  
*Synchaeta pectinata* Ehrbg.  
 — *tremula* Ehrbg.  
 — *stylata* Wierz.  
 — *oblonga* Ehrbg.  
*Polyarthra platyptera* Ehrbg.  
*Anarthra aptera* Hood.  
*Diurella stylata* Eyfert.  
*Rattullus cylindricus* Imh.  
 — *pusillus* Lauterborn.  
*Euchlanis oropha* Gosse.  
*Ascomorpha agilis* Zach.  
*Sacculus viridis* Gosse.  
*Anapus testudo* Lauterborn.  
 — *ovalis* Bergendal.  
*Hydatina senta* Ehrbg.  
*Rhinops vitrea* Hudson.  
*Brachionus pala* Ehrbg.  
 — *angularis* Gosse.  
 — *urceolaris* O. F. Müller.  
*Schizocerca diversicornis* Daday.  
*Anuræa aculeata* Ehrbg.  
 — *cochlearis* Gosse.  
*Anuræopsis hypelasma* (Gosse).  
*Notholca acuminata* Ehrbg.
- Notholca longispina* Kell.  
*Gastropus hystopus* Ehrbg.  
 — *minor* Rousselet.  
 — *stylifer* Imhof.  
*Ploesoma triacantha* (Bergendal).  
 — *Hudsoni* Imhof.  
*Asplanchnopus myrmeleo*.  
*Asplanchna Sieboldi* Leydig.  
 — *Brightwelli* Gosse.  
 — *amphora* Hudson.  
 — *prionota* Gosse.  
*Conochilus volvox* Ehrbg.  
 — *unicornis* Rousselet.  
*Conochiloides natans* (Seligo).  
*Triarthra longiseta* Ehrbg.  
 — *brachiata* Rousselet.  
 — *breviseta* Gosse.  
*Pedalion mirum* Hudson.  
*Pompholyx complanata* Gosse.  
 — *sulcata* Gosse.  
*Floscularia libera* Zacharias.  
 — *pelagica* Rousselet.  
*Actinurus neptunius* Ehrbg.  
*Rotifer macroceros* Gosse.  
 — *macrurus* Ehrbg.

With regard to the Crustacea it is most probably the group which possesses most of those species which either belong only to the lake plancton or only exceptionally occur in ponds, (*Limnosida*, *Daphnella*, *Bythotrephes*, several races of *Daphnia* and *Hyalodaphnia*; *Bosmina coregoni*), and further species which are strictly limited to very little ponds or pools (*D. magna*; *D. Atkinsoni*, *Diaptomus* species). On the other hand the pond plancton is characterized by the great rôle which the *Ceriodaphnia* species play. Of the six *Ceriodaphnia* species, which we have in Denmark, it is in reality only two which occur in the plancton, viz. *C. pulchella* and *C. quadrangula*. Of these *C. quadrangula* is the most planctonic; it occurs in several small lakes e. g. in Gribssø, producing the greater part of the plancton volumina during the whole year. Here as in one of our largest lakes Mossø (max. depth 30 m.) it occurs in the var. *hamata*. — The *Hyalodaphnia* may very well occur in ponds, but then commonly in peculiar dwarf races with only a very inconspicuous seasonal variation. The races of *D. hyalina* are more common, they are often superseded by *D. pulex* in small ponds; in our country *B. coregoni* has never been

found in ponds; it does not occur in a large pond like the Frederiksborg Castle Lake. Instead of it we have *B. longirostris*, which plays a very conspicuous rôle in many ponds. *Holopedium gibberum* is extremely rare in Denmark; hitherto we have only found it in three localities, two of which may be regarded as small lakes; one of them (at Hellebæk) is only a pond with a depth of 2—3 m. Even if *Leptodora hyalina* is mainly a lake form it may still occur in water volumes, whose depth is only about 3 m. (Frederiksborg Castle Lake). Of the pronounced lake forms *Daphnella brachyra* may occur even in ponds as small as Funke Pond, from which it has now disappeared.

Of the Copepoda there occur in the Baltic lakes in the first place the two *Diaptomus* species *D. gracilis* and *graciloides*; the *Hetercope* and *Eurytemora* species are rare; the two *Diaptomus* species also occur in ponds, *D. graciloides* seems to be the most pronounced lake form. In very small ponds, often such as dry up totally, *D. castor*, *vulgaris*, *coeruleus* and *superbus* may be found. Of these *D. castor* is a pronounced spring form, occurring in drying pools. Of the *Cyclops* species *C. oithonoides* and *C. strenuus* belong to the lake plancton, but may also occur in ponds; especially *C. strenuus*. Here they are often found together with *C. Leuckhardtii* and *C. albidus*, which of all *Cyclops* species seem to be those which are best able to live beyond the vegetation; they may also occur in the pelagic region of larger lakes.

No *Harpacticidæ* are found in the plancton of either lakes or ponds, but now and then the *Ergasilus* species may occur in both localities in a fairly great number; owing to their brilliant blue colour, they are easily recognizable.

Further a few other organisms belong to the plancton in lakes as well as in ponds: *Argulus foliaceus*, *Atax crassipes* and *Corethra* larvæ. Now and then *Argulus* is a very common organism in pond-lakes during summer. The *Corethra* larvæ are pronounced pelagic organisms. They stand in enormous quantities in the deeper water-layers of our largest lakes, and in some ponds may fill the water with incredible masses; so large that a single haul may give them in handfuls. Some *Hydrachnidæ*, *Atax crassipes* a. o., play a considerable rôle in the pelagic region of some smaller ponds e. g. in Gripsø.

2. My plancton investigations of the Danish lakes (1904—1908) have shown that the composition of the plancton in our lakes is almost the same in all the lakes; the maxima which the species reach in the different lakes may differ, but all in all most of the species are found in all the lakes explored. Species which are only known from a single lake are few.

With regard to the pond-plancton, this conformity is by no means the rule. Within a radius of only a few kilometres we have, in an explored area in ca. 50 ponds, during the summer-months, the greatest variety in the composition of the pond-plancton. This seems to be the case everywhere in our country. I have examined this matter in North Seeland near Hillerød; in the central part of Seeland near Sorø, in the Silkeborg and Hald-Viborg districts in Jutland. The result is that,

on the very same day, every pond, so to speak everywhere, has its own plancton, composed of organisms several of which are peculiar to that single pond. Thorough explorations show that a great many pond-planctonts are found which are only known from a single pond, a fact which will be well known to all investigators of the pond-fauna and pond flora abroad. This will especially be admitted by the algologists, who have studied the Chlorophyceae, Volvocales and Flagellata in smaller ponds; but also the students of rotifer-life in ponds will admit the correctness of this assertion. The variation may go so far that, in an old peatbog, every little hole may at a given moment have its own fauna and flora. A more thorough exploration in this case will show that the phenomenon is due to the fact that many of the planctonts, common to the whole bog, do not reach their maxima simultaneously but successively; nevertheless there will always remain some rare species which, year after year, can only be found in a single hole.

3. Regular investigations further show that this great variation in the composition of the pond-plancton only occurs in the summer months. It begins to manifest itself two or three weeks after the loosening of the ice; it is at its height at the highest summer temperature in July—August; then it diminishes in November and is almost obliterated shortly before ice covers the water.

4. If by the term winter-plancton we understand the plancton which is present at a temperature of  $+3$  before the ice-covering, during ice-covering and from the loosening of the ice to  $+3^{\circ}\text{C}$ ., we can substantiate another great difference between lake and pond-plancton. The winter-plancton of our lakes is a combination of phyto- and zooplancton, the phytoplankton preponderating in mild winters; the winter-plancton of the ponds is often an almost pure zooplancton. In the first place this is due to the fact that the diatoms which often in lakes may develop huge maxima at a temperature near zero so to speak play no rôle in the pond-plancton and are almost always absent in the real ponds. This holds good especially with regard to the *Melosira*, just those diatoms which predominate in our lakes during winter. *Asterionella* which is the only diatom which may form large maxima in ponds, has not its maximum before May. With regard to the Cyanophyceae, *Coelosphaerium Kützingianum* may still be rather common in December, but it almost always disappears before the ice-covering. All the small Chlorophyceae have all their maxima during the summer months; some of the Volvocales (*Eudorina*, *Pandorina*) may occur singly at a temperature round zero. It is only among the Flagellata that we may, shortly before the ice-covering, find rather conspicuous maxima; in mild winters they are able to develop maxima in January—February. This holds good especially for *Dinobryum*, *Synura uvella*, *Uroglena volvox*, some *Peridinium* species, but not for the *Mallomonas* species where maxima appear at much higher temperatures. This is also the case with almost all other Flagellata belonging to the free central parts of our ponds. Many of them are found till the ponds are icebound; but during a frost period, even if it is short, their number diminishes and immediately after the loosening of the ice, they play no conspicuous rôle as far as hitherto known.

Practically speaking the winter plankton of our ponds consists almost exclusively of zooplankton and in contradistinction to the summer plankton it is homogeneous almost everywhere.

Of the three main components, Infusoria, Crustacea and Rotifera, the Infusoria only play a very inconspicuous rôle during winter; *Codonella lacustris* and *Tintinnidium fluviatile* are the only ones occurring. The Crustacea are most predominant. The pronounced pond forms of the genus *Daphnia*, *D. magna*, *D. pulex* and *D. Atkinsoni* have commonly made their ephippia before the water is covered with ice; the same is the case with the pond races of *D. longispina*, the *Hyalodaphnia* and the *Ceriodaphnia* species. Nevertheless locally, as well as temporally, varying from year to year, some specimens of all these species occur sporadically during winter. Of real significance among the Cladocera is in the first place *B. longirostris*, with us mainly in the form *cornuta* Jurine. It may have large maxima immediately before the covering of the water with ice and be abundant below the ice. In the different ponds great differences prevail. In some of them and in some years it totally disappears during the freezing period, in others it is abundant immediately after the loosening of the ice. Even after an ice-period of more than 100 days it has been pointed out that in samples taken in openings of the ice, it is one of the main forms.

With regard to the Copepoda only two species predominate in the pond-plankton during winter: *Diaptomus gracilis* and *Cyclops strenuus*; the first-named as a rule not in too small ponds; when it occurs, it is commonly the main form in winter samples. It and *C. strenuus* together form the greatest quantities of the zooplankton in our ponds during winter; of much smaller significance are *C. Leuckardtii*, *C. albidus* and in the larger ponds *C. oithonoides*. — The rotifers of the pond-plankton during winter consist of the following species:

<i>Anuræa aculeata.</i>	<i>Notholca acuminata.</i>
— <i>cochlearis.</i>	<i>Polyarthra platyptera.</i>
<i>Asplanchna priodonta.</i>	<i>Synchaeta tremula.</i>
<i>Brachionus pala.</i>	— <i>pectinata.</i>
— <i>angularis.</i>	<i>Triarthra longisetata.</i>
<i>Notholca scapha.</i>	

The lists also show the species *Ascomorpha agilis*, *Gastropus hyptotus*, *Rattulus bicornis*, *Rhinops vitrea* at temperatures + 3 — 0 — + 3, but they only occur sporadically and not every year. The other species are present below the ice during all winters and almost in all ponds, the *Notholca*-species only in small number, and the same is often the case with *Asplanchna priodonta*, but the other species, the *Anuræa*, *Brachionus* and *Synchaeta*-species, *Polyarthra* and *Triarthra* are almost always present everywhere. Characteristic of these eight species is furthermore the fact that during winter they hardly ever have conspicuous maxima; they have had their sexual periods before the water was covered with ice, or they are about to have a new one immediately after the loosening of the ice. During the autumnal sexual period a great amount



of resting eggs have been developed and deposited, but after the death of the mictic females, some amictic ones have been preserved, and it is these females which at a very low temperature continue the parthenogenetic propagation. In reality this proceeds very slowly; in severe winters it is brought to a standstill; this may cause the stock of amictic females to die out, so that new maxima in the spring are only developed from the material hatched from resting eggs. In very mild winters when the ponds are open almost the whole year round and the temperature of the water is about 4—0° C. the amictic females may really develop very large maxima. A very few mictic females carrying male eggs may occur, but resting-eggs are very rarely observed, and a conspicuous sexual period is not developed.

From a biological point of view there is in reality no great difference between a resting egg and a parthenogenetic egg developing at temperatures round zero; during the last part of a long freezing period the winter planctons carry eggs but never young ones with developed wheel-organs; most probably the specimens live for many weeks and carry the eggs as long.

It may be added that the above-named species are just the same which are mentioned as main forms in the arctic and high alpine lake plancton. To these may further be added *Conochilus volvox*, *Notholca longispina* and *Ploesoma Hudsoni*, which all seem to play a conspicuous rôle in high alpine lakes. Of these *Conochilus volvox* may be found with rather high maxima at a temperature near 5° C., but then it seems to disappear. Curiously enough *Notholca longispina* is never in our country found before spring; it disappears in October. It has its maximum in May—June, whereupon it may be found sporadically during the summer, now and then attaining a modest maximum in the autumn. *Ploesoma Hudsoni* which is a typical summer form with us, plays a conspicuous rôle in the arctic and alpine lakes; in our lakes it appears at a temperature of 10—12° and disappears at the same temperature in the latter part of October; only a few times have I observed the species in the latter part of November at a temperature of + 5. —

5. Even if the amount of phytoplankton differs much locally and temporally in our country, where the fields are manured in a very high degree, where the precipitation, before reaching the stagnant water, is mixed with enormous amounts of organic matter, and where the lakes and ponds are small and shallow and the water-masses almost always coloured by phytoplankton, the amount of this as a source of nourishment for the other plancton organisms is almost always enormous; from the very moment when the ice has melted till the waters again freeze, often not until January, the great maxima of the different phytoplanktons follow each other. That the amount of phytoplankton from March to January should be so greatly reduced, that it should in any way be able to make its influence felt upon the amount of zooplankton, its sexuality and its seasonal and local variations, is highly improbable. He who maintains that the *Hyalodaphnia* reduce their helms in September owing to a diminution in the amount of phytoplankton, i. e. in the amount of nutriment, might with equal right maintain that the nightingales leave our forests in the first

part of August, because they cannot any longer get a sufficient amount of insects to stay their hunger. —

6. The plancton explorations in 1904—1908 have shown that the perennial plancton Daphnids of the lakes are subject to great local and seasonal variations; the pond explorations show that this is only in much slighter degree the case with the Cladocera in the pond plancton. The seasonal variation of the *Ceriodaphnia* is extremely small, almost problematic, the *Hyalodaphnia*, as is often the case with pond-races, have none or a very slight seasonal variation, *B. coregoni* is absent in ponds, and the seasonal variation of *B. longirostris* is but small. The fact is in accordance with the supposition that the seasonal variation partly depends upon parthenogenetic propagation, this being most pronounced among the lake daphnids, which are often acyclic, whereas sexual periods with following amphimixis, once or twice a year, are the rule for the pond daphnids.

Curiously enough it seems that all this is opposite in the Rotifera. Precisely some of the main genera of the pond-plancton, the *Anuræa*, *Brachionus* and *Notholca*, are subject to a pronounced seasonal and local variation. With a few exceptions it almost seems that seasonal variation is totally unknown among the rotifers from the pelagic region of larger lakes. All authors agree that the cyclomorphoses of the *Anuræa* mainly known from the studies of LAUTERBORN are unknown from larger lakes.

Here it shall only be added that *Anuræa tecta* is regarded as a species. —

The *Anuræa* and *Brachionus* vary from pond to pond, almost every pond has its own race; in lakes the local variation is but small. Add to this that among different genera of Rotifera we find forms which unquestionably are very nearly related to each other, but may nevertheless be regarded as distinct species, or sub-species, and which seem to arrange themselves in form-series, the single members of which have a specific range. These sub-species or "petites espèces" are limited to ponds of a specific nature, drying ponds, Sphagnum pools, manure pools etc.; it is especially the genera *Anuræa*, *Synchaeta*, *Polyarthra*, *Triarthra* which exhibit examples of this. — It is here as if locally separated specimens, exposed to extreme variations in external conditions, have caused the formation of petites espèces. Unquestionably these phenomena are not in accordance with the supposition that the great power of variation partly depends upon parthenogenetic propagation and wanting amphimixis. All these forms have well marked sexual periods; they are either mono- or dicyclic and now and then polycyclic.

On the other hand the great variation of the pond rotifers is in accordance with very many other pond organisms. Whether we study *Mollusca*, *Dytiscidæ*, *Notonectidæ*, our *Donacia*-species, the colours and patterns of some of our frogs, especially *Rana esculenta* or *Triton cristatus*, we shall find that they are all subject to great local variation. It is as if every pond so to speak has its own race; in many cases a specialist who knows its area, can tell to which pond the said animal belongs. In reality the fact is easily understood. The animals are so to speak tied to

the pond in which they are born; as most of the ponds have no affluxes and are only fed directly by the precipitation, the possibility of a supply of new blood is but slight, and interbreeding will be the result; through accumulation small modifications caused by external conditions will be preserved and cause racial characteristics. —

7. If furthermore we study pond life in the very same ponds, but during a series of years, it becomes obvious that these great variations in the composition of the fauna hold good in great degree not only horizontally through space but also vertically through time.

Nowhere do the variations in the composition of the fauna seem to be so great from year to year as in ponds. It is a well known fact that Phyllopods may one year be very numerous in a given pond, in the next year or even in a series of years not a single specimen can be found. This holds good especially for *Branchipus* and *Apus*. In North Seeland we can speak of *Limnetis*-years, i. e. years when *Limnetis* is found in numerous ponds; then for a series of years it will be impossible to get a single one; my studies on *Planaria* (*Mesostoma lingua*), Cladocera, Rotifera, Flagellata, Ostracoda, *Diatomus*-species, Hydrachnida have all shown the same fact. A species may be abundant in a pond one year, disappear for three or four years, and then suddenly reappear. Furthermore explorations carried on year after year in the same pond show that species which are constant temporally, may live their life in the same locality in different manners in the different years. One year the species will propagate monocyclically, the next dicyclically, in another again the formation of resting-eggs is almost stopped; the sexual period may be much displaced, in one year forward, in another backward. Owing to the great variation in the composition of the pond plancton from year to year, especially of the nannoplancton, the diet differs enormously and exerts its influence upon the ripening of the sexual products. In one year species have completed their development before the ponds are covered with ice, in others they are forced to hibernate as larvæ below the ice (frogs, salamanders) resulting in tendency to Neotæni in one year, but not in others.

What is here indicated will, it is to be hoped, be more fully treated later. It is sufficient to point out, what is, by the way, a well-known fact, that the pond fauna is extremely variable, locally as well as temporally. It is just this almost incredible variation which makes the study of this fauna at the same time so attractive and so difficult. —

## Chapter IV.

## Some Remarks with Regard to the thermal and chemical Peculiarities of the Water in our Ponds.

## a. General Remarks.

Of course all who have studied one of the groups of animals or plants belonging to the pond fauna have tried, in the varying life conditions which the ponds offer the organisms, to find the causes which govern the great biological and morphological variations.

With regard to the Cladocera, WAGLER has very thoroughly tried, by experiments in the laboratory, to elucidate the influences of variations in external conditions upon the organisms, biologically as well as morphologically.

The main result, especially with regard to *Daphnia cucullata* was as follows: "Die grosse Masse der Teiche und Seen bleibt gewöhnlich in ihrem Salzgehalt weit unter den Maximaldosen die als erträglich für *D. cucullata* angesehen werden können."

This result most probably holds good also for many other animal pond organisms. Having no saline ponds in my country I was forced to suppose that, apart from the temporary ponds which only possess water 5—6 weeks in spring, the life conditions in the others were all in all of so uniform a character that the variation in the composition of the pond fauna and the great variations biologically and perhaps also morphologically with regard to single components in different ponds, could only with difficulty be interpreted from temporal and local variations in the external medium.

All that could be pointed out was that we may most probably refer our ponds to two types: the acid and the alkaline ones. The fauna in the first-named, characterized by its very brown water, and probably by its high acidity, had a peculiar character differing from the other pond fauna in our country. This fauna was best characterized by all those organisms which were wanting, not so much by organisms which were only to be found in ponds of this nature. Very characteristic is the total lack of all mollusca, of a long series of species of insects especially Phryganids, of Cladocera, Rotifera and Hydrachnidae. Characteristic of these brown waters were especially *Holopedium gibberum*, some *Chironomid* larvæ, *Latona setifera*, many *lynceid* Cladocera, the ephemerid larvæ *Leptophlebia* and especially in small water areas *Anuræa serrulata*; in bog-moors a series of *Notommatidæ*, especially belonging to the genera *Copeus*, *Triphylus*, *Eosphora* o. a. —

In my area of exploration, and I may say in our whole country, we have many bogs and moors; most of the water-masses belonging to them are artificial ones, such as pit holes; all of them are therefore relatively small; of larger natural

water-areas, smaller lakes with pithy water, we only possess very few, in the islands most probably only Gripsø and in Jutland a few more (especially the Øxø).

The main part of our ponds and smaller water areas belong to quite another type, mainly neutral or alkaline, extremely rich in organic matter; the water is green or yellowish green with the colour determined by the colour of the chromatophores of those plancton algæ, which prevail in the water area at a given moment. There is no doubt that the fauna in acid waters, at all events in our country, is of a relatively uniform composition, and that its components, locally and temporally, live a relatively monotonous life. The enormous variations in the composition of the fauna and the variations in life conditions for the individual members, locally as well temporally, belong to the small, alkaline waters.

This impression, the result of many years' study, has been confirmed by others with a different scientific training, and who have carried their investigations, starting from other points of view, to a much higher degree of perfection.

The more we study nature, the clearer it will be that it is a very dangerous thing to press nature into schemata, divide our observations into categories and furnish them with a lot of fine jingling names. All these boundaries, limiting these categories, do not exist in Nature, they are only to a very slight degree necessary and the making of them has taken a lot of time which could have been better employed.

That the former of the two groups of water areas in the new terminology is to be designated as dystrophic and oligotrophic, the last eutrophic, I know very well; these, as well as many other new limnological names, may very well be used; only we must remember that science has not moved a single cock's stride forward owing to this terminology. The main result at which I had arrived, that there was a significant difference between soft (acid) and hard (alkaline) water rotifers, furthermore that the fauna showed many problems which could not be explained by and did not agree with the variations in the amount of calcium carbonate in solution, the amount of which in our country mainly determines the softness and hardness of the water, I found again in HARRINGS and MYERS Tom IV on the rotifer fauna of Wisconsin (1928 p. 672). The authors have carried their investigations further than I and arrived at the result that it is the hydrogen ion concentration which directly determines the rotifer distribution. According to them it is neutrality, or pH 7.0, which seems to be the dividing line. —

Above this in alkaline waters all the "cosmopolitan" rotifers are found in enormous numbers but in relatively few species. A complete change occurs when the reaction drops below pH 7.0, the number of individuals is then much smaller, but there seems to be no end to the number of species. This continues until the acidity becomes very pronounced, and at pH 4.0 but very few species of rotifers remain. From their areas of investigation HARRING and MYERS give good examples of the correctness of this sentence. They maintain that the pH range of individual

species as a rule appears to be quite narrow, from 2–3 units of pH; the most striking fact observed is the total disappearance of the genus *Brachionus* in acid waters, with the single exception of *B. polyacanthus*; furthermore of species belonging to the same genus, one of which is ubiquitous in alkaline waters (*Euchlanis triquetra*) another *E. pellucida* in acid water. Furthermore that a long series of species, hitherto regarded as rare, are typical acid-water animals, and only hitherto rarely found because they were not searched for where their real home was. We shall return to the question of the significance of the pH value for the distribution of the Rotifera later on.

#### b. Some Remarks on the Temperature of our Ponds.

As mentioned above, most of my ponds belong to the eutrophic (alkaline) type. Precisely in this type the variation in the composition of the pond fauna and in the life of its single components was enormous. Searching for external factors which could be supposed in some way to be made responsible for this great variation, I found one which in countries with an insular climate has a much greater significance than hitherto known; it may especially be used to explain the great variation in habits of life in different years.

Already as a young student I had noted the remarkable phenomenon that our ponds and lakes might in one year be open almost the whole year, in another frozen over for many months. This made me for the series of years, 1897 to 1929, note the day when the ponds near Hillerød were ice-covered and the day when they thawed again; my observations from 1914–1916 have been lost.

All these ponds lie within a circle with Hillerød as the centre and with a radius of 3–4 kilom. The number of ponds amounts to 25–30 every year. The observations are not equally valuable in all the years of observation; some years the ponds were icebound and again thawed so many times that it was almost impossible to get the right number for the icebound days. Nevertheless, of the 28 years of observation, the 17, at all events, may be said to contain statements which are so trustworthy that the errors most probably do not exceed a few days. The ponds on which the observations have been made, are almost the same every year, i. e. the ponds which I have used for my many different observations relating to Dytiscidæ, Cladocera, Culicidæ, Hydrachnidæ, Rotifera etc. Their depth is always small, from a few decimetres to about 2 m. We will first discuss the ponds which have water the whole year round and then the temporary pools, which are only water-filled for a few weeks, mainly in the spring and early summer.

The observations show that during the period 1897–1924, during 22 years of observation, the ponds have been icebound on an average for about 80 days a year; 60–70 may be the commonest number. The most interesting fact is, however, that the pronounced insular climate of our country manifests itself so mark-

edly with regard to the freezing periods of our freshwaters, that there are years when the ponds are icebound only for 8 days, and others in which they are icebound for 146 days i. e. almost for  $\frac{1}{3}$  of a year.

The number of icebound days depends in the first place on whether or not the ponds have had a freezing period in November, December; in years in which this period is wanting, the number of icebound days is as a rule smaller. The period commonly begins during the days  $\frac{2}{11}$ — $\frac{15}{11}$ ; it may last till the first part of January, it is only very rarely continuous; as a rule the ponds freeze over and thaw two or three, often many, times before January; in many winters (1897—1898; 1898—1899; 1910—1911; 1913—1914; 1916—1917; 1918—1919) the ponds are open during the whole period to  $\frac{1}{1}$ — $\frac{15}{1}$ ; occasionally ponds do not freeze again until after  $\frac{15}{1}$ . As a rule the more stable period does not begin until January or in the last days of December (1906—1907; 1908—1909; 1909—1910; 1910—1911; 1911—1912; 1913—1914 and in almost all the years from 1916 to 1923). — This period is only very rarely, as is the case with the preceding one, divided into a series of icebound days succeeded by a series of icefree ones, it is as a rule continuous and when the ponds thaw, it is as a rule definitely. When the ponds have thawed in spring, they only very rarely freeze over again; this has only happened in 1911—1912 and 1921—1922. The period in which the ponds are icefree is commonly restricted to the days  $\frac{1}{4}$  to  $\frac{15}{4}$ .

In a few years we have no alternating icebound and icefree periods in autumn, but the main freezing period begins in the first days of December and then lasts the whole winter. This was the case in 1899—1900; 1905—1906. The main freezing period which commonly lasts from the first part of January to the first part of April only rarely extends over the whole period (1899—1900; 1905—1906; 1906—1907; 1908—1909; 1916—1917) it is very often restricted to only a fraction of this period, and may then be displaced either forwards or backwards; in 1897—1898 to the last part of March; in 1909—1910 mainly to February and the first part of March; in 1913—1914 to the last half of January and February; the period is the same in 1920—1921. The main period may really be rather short, only 30—56 days, but in relatively many winters (7) its number lies about 100 and may reach 120 (1905—1906 and 1928—1929).

The peculiar thing is that the greatest number of icebound days is by no means reached in those winters which are regarded as the coldest, and whose mean temperature of the air is lowest.

For if a freezing period in November begins with rather high degrees of frost, and these act over a period of 10—14 days, the ice is then so thick that the temperature of the air, even if it is above zero during the whole of December, is incapable of thawing the ice; this is especially the case in winters with heavy fogs, drizzling rain, very little sun and feeble winds; in other words, winters which tempt *Eranthis* and *Galanthus* to sprout in our gardens but are unable to give our small waters spring conditions.

In this way the ponds may be frozen from the middle of November to April, even if December and a good deal of January have temperatures above zero (c. 140 days).

In my area of exploration most of the ponds freeze simultaneously, at all events in the course of only 3—4 days; this is especially the case when the freezing period sets in with sudden rather strong frost — 6 — 7° C. On the other hand, if we have only a slight night frost, the specific conditions of the ponds assert themselves, and these may give a rather conspicuous difference in the freezing data; ponds lying in open terrain will, if the wind is strong during the freezing period, freeze over later than those lying in wind-protected localities. Furthermore, when the period begins with a sudden snow-storm, in which enormous quantities of snow are poured down in the small basins of water, the temperature of the water will in a few hours be lowered to zero; a few degrees below zero then cause the freezing of the ponds. In larger ponds this will not be the case, because these ponds still possess an excess of specific heat which cannot be lowered as fast as that of the small ponds. As furthermore the ice which is formed on the small ponds at the same air temperature gets thicker than on larger ponds, the small ponds may get a greater number of icebound days than the larger ones. Nevertheless, as mentioned above, the difference in dates for the freezing over of our ponds is commonly but slight. That this is in the first place connected with the fact that the differences in the position of the ponds above sea-level are insignificant in our country needs no further explanation.

Whereas the freezing data for our ponds in the autumn are practically the same, this is not the case with the days in which the ponds thaw in spring. We may here have a period, often above two weeks, in which we find some ponds icefree, others icebound.

It is especially the shady wind-protected ponds which thaw latest; especially the forest ponds may retain the ice longest. Here the ice lies slowly decaying; a warm spring rain is the best means to melt it; on larger wind-open ponds, a strong spring wind can set the whole of the brash ice in an undulating motion and in the course of a few hours it is able to sweep the whole mass ashore. There have been years in North Seeland when the forest ponds have had ice for 3 weeks after all ponds of the open land had been icefree.

An element contributing to the melting of the ice, is the process of fermentation going on in our ponds which are overfilled with decaying vegetation. Already in 1912 (p. 272) I have shown that in severe winters the temperature in icecovered ponds, covered during summer with vegetation, rose at the bottom; the water immediately below the ice could in such ponds reach 2.4° C.; at the bottom it was 4.2 on  $^{27/2}$  1909 and 5 on  $^{13/3}$ .

The high temperatures below the ice cause melting processes to take place which give the underside of the ice a peculiar pock-marked appearance.

Where floating leaves of *Potamogeton* and *Nymphæa aceæ* are frozen in the ice,



the dark surfaces of the leaves will absorb the sunbeams more than the surrounding ice, and hollows from above eat their way through the ice; now and then the floating leaves of the vegetation are caught in the ice before it is dead, and the assimilation then goes on from the leaves giving rise to airbubbles which eat their way through the ice. Every sunny winterday will give rise to an airbubble, and in this way "money piles" of airbubbles will appear, every bubble indicating a sunny day. Later on these bubbles will fuse together and the result will be a canal through the ice. These are also formed by the bubbles of methane, which rise from the bottom to the under side of the ice; being more heated by the sunshine than the surrounding ice, they slowly eat their way through the ice. In this way the ice is filled with greater and smaller canals, so that it may disappear quite suddenly, if only a wind can reach the surface. In the heated littoral zone the melting of the broken ice masses takes place in the course of a few hours.

The smaller the ponds are, the more decided an influence has the number of hours of sunshine on the temperature of the pond and so also upon its organisms. This holds good especially if the ponds are either covered with vegetation or furnished with large quantities of plancton. Upon days with high temperatures overshadowed ponds and ponds lying in bright sunshine often show a temperature difference of 7–8° C. (from 17 to 24° C.). In the course of the night the difference will be come nil and on rainy over-clouded days it is untraceable. —

As far as I know FOREL was the first to point out that dirty waters are warmer than clear ones; this is due to the fact that the floating detritus particles are heated more than the surrounding waters, which, again, are heated by the heat radiating from them. Ponds crowded with plancton organisms, especially *Cyanophyceae* behave like dirty waters. In ponds with high *Cyanophyceae* maxima the temperature may vary on two successive summer days in accordance with the amount of clouds and number of hours with bright sunshine from 15–28° C.; in the course of one single day and night period a pond may pass through this whole scale. — In calm weather the temperature of the water in *Cyanophyceae* ponds, especially below a thick *Cyanophyceae* cover, may rise high above the air temperature; we may here find a temperature of + 27 or 28° C. whereas ponds without *Cyanophyceae* maxima have only 23° C. —

Already in 1912 (p. 287) I pointed out how high the temperature may rise in early spring on sunny days on the sheltered southward-exposed sides of ice-bound ponds; only two meters from the ice in the ice-free border, 17° C. (<sup>7</sup>/<sub>4</sub> 1909) have been measured. In Funke pond at <sup>19</sup>/<sub>3</sub> 1910 at an air-temperature of 4° C. the temperature at the southwards-exposed sides of the pond was 14° C. at the northward exposed side 4–5°. The pond had been open about 8 days. —

On lake borders with a southern exposure we have spring, on the northern

side thick ice and winter. These observations have subsequently been corroborated by others (e. g. Dr. KAARE STRØM 1927 a p. 53, 1927 b p. 343, 1928 p. 329); they have been used to explain the peculiar fact that the same layers in our marsh and peat bogs may contain arctic land plants such as *Dryas* and *Salix polaris* and simultaneously water-plants and water-animals (*Potamogeton* and *Limnæa*) which require much higher temperatures, a phenomenon which has rather puzzled the glacial geologist, and which, according to the statements of NATHORST (1914 p.287) a. o. finds its natural explanation in this way.

It will be understood that the above-named peculiarities relating to the temperature of our small waters may exert a very great influence on the fresh-water fauna, its distribution and its mode of life. Shadowed forest ponds which will commonly be ice-covered about three weeks longer than those of the open country, and which never attain the high summer temperature mentioned above, have a fauna and flora differing from the last-named.

There is still a point with regard to the temperature of our ponds and smaller lakes which must not be omitted if we want to understand the composition of our pond fauna and flora. The sheltered small creeks and coves of our small waters are perhaps those localities in our country which will attain the highest temperature on sunny, warm, and calm days. Often in the water rim it may reach 28°—30° C. Nowhere in our country does the vegetation attain such a luxuriant development as just here; only in localities of this nature is *Hydrocharis morsus ranae* able to produce ripe fruits, many warm-loving plants of our swamp and moor-flora are restricted to these sheltered creeks. But quite the same is the case with organisms belonging to the fresh-water fauna and which have their northern limits of distribution just in our latitudes; this is the case e. g. with the Odonat *Epithea bimaculata*, several *Phryganidæ*, *Ranatra*, *Bombinator igneus*, *Rana esculenta* and very many members of the microscopical pond fauna; the Rotifera form no exception. It is in localities of this nature that we find a good deal of those species, which are rare in our country as well as in others, e. g. *Asplanchnopus myrmeleo*, *Noteus militaris*, *Stephanoceros Eichhornii* and many of the other sessile rotifers. It is here too, I suppose, that *Notops brachionus* will once be found. All these forms are not to be found in the cold overshadowed ponds. If we want to understand the great variation in the fauna of our ponds, this fact must not be forgotten. —

Furthermore, if we want to understand the great variations in the life of the pond fauna from year to year, it is in the first place the number of days the pond has been frozen over in the said year which must be considered. The life conditions, especially the respiratory conditions, differ extremely during winter from pond to pond and from year to year. In late autumn we see those insects which use atmospheric air to satisfy their respiratory needs, during night fly in search of ponds rich in vegetation.

During winter, below the ice and especially upon sunny days, the plants produce oxygen, which is drawn directly into the respiratory system through the

spiracles as airbubbles. In severe winters the respiratory conditions are very hard in our ponds; numbers of *Dytiscidæ* *Notonectidæ*, furthermore *Limnæa* which hibernate during winter with lungs filled with water, using their lungs as water-lungs, are found dead near the shores after the ice has thawed. The above-named holes in the ice are of importance with regard to the respiratory conditions of the fresh-water fauna; when the ponds are near thawing, we often find members of the winter pond plancton *Diatomus*, *Cyclops* and *Anuræa* in the pools of water on the surface of the ice. —

The heating zone in early spring on the sides of the ponds with a southern exposure is of the greatest importance for the fauna. Before the ice has melted a great part of it floats to the water rim, on the southward sides of the pond at that time harbouring an enormous lot of organisms, which here, in the warm water, either get their sexual products ripened, or get food enough, which allows growth, resulting in moults and shortening of the period preceding the ripe stage. But in just the same locality we also find the resting stages, the hibernating buds of the vegetation of *Myriophyllum*, *Hydrocharis*, *Stratiotes* a. o. as well as the statoblasts of the Bryozoa, the gemmulae of the Spongillidæ, the ephippia of the Cladocera and resting eggs of the Rotifera. On sunny days they lie here a few decimetres from the ice borders, in water with a temperature of about 10—12° C. Here, in the early spring, a great deal of the spring plancton of our ponds is born and shortly afterwards carried out into the free water-layers. The number of days in which the ponds have been frozen over is a contributory factor to how many parthenogenetic generations a species may get before the sexual period; in some years only a very few, in others a long series. It is the same factor which in part determines if a species in a certain locality and a certain year shall hibernate solely in the resting stage or also as free-swimming organisms with a very restricted parthenogenetic propagation. With regard to the rotifers it is again the same factor which determines if life in the early spring shall develop solely from the resting-eggs or also from hibernating amictic females, or with regard to the Cladocera from hibernating females with a suddenly augmenting enormous power of propagation in the early spring or solely from ephippia. It is the same factor which decides if a species in a certain year and in a certain locality shall propagate polycyclically, dicyclically or monocyclically. Owing to the amount of heat-units which the organisms require, it is again, the same factor which partly determines the composition of the summer plancton, in one year giving extremely good developmental conditions to one organism, and in another to another; when in a pond a form is the main form the one year and totally wanting the next, I suppose that this may be due to the temperature and especially to how severe the winter has been. In mild winters in ponds which have been open in January—February I have seen *Triarthra longiseta*, *Brachionus angularis* and *pala* as the main forms in the zooplankton until the latter part of April and they have had large maxima at temperatures of +4 — 0 — +4° C. Furthermore, in the same ponds, in years in which the ice did not

disappear until April, I have seen that the same species were relatively rare in April—May and at the moment when the *Cyanophyceae*, the *Hyalodaphnia* and *Asplanchna priodonta* got huge maxima, they totally disappeared without getting either maxima or sexual periods before October. — During winters when the ponds are open the whole of December the above-named species may at temperatures  $+4 - 0 - +4$  have a very lively parthenogenetic propagation; mictic female may appear and also males, but it seems as if resting-eggs are very rarely formed. A short period of icecovering (5—7 days) makes no difference, the species are as common before the icecovering period as after.

Temporary pools. After winters with much snow, the fields and the ground in our forests may be covered with numerous temporary pools, the water of which derives from the melting snow blown into the small depressions in the ground. Most of them dry up in May—June and get no water again until next spring. They harbour a rich fauna which passes the greater part of the year on dry land, as resting stages between withering leaves or covered by grass or the forest flora.

In many cases these temporary pools begin the winter period without a drop of water, in others in which the winters begin with snow-storms followed by thaw, they are, in late autumn, filled with water deriving from the melting snow; they are then in November—December full of water. Then when winter sets in again, the water is covered with ice and often freezes to the bottom. In some years the pools may thaw and freeze several times during the winter, in others they may be frozen over while all other ponds are icefree, and in this way get a greater number of icebound days than all the other ponds in our country, and much greater than might be expected in a country with so pronounced an insular climate.

In these ponds we find some of our rarest Rotifera. They behave like all the other components of the fauna of temporary pools, they are common one year, and the next are not to be found. —

In the above-named great variation in the amount of water at different periods during the winter, and in the length of the periods in which they have been icebound, I suppose we have some of the traits which cause the great irregularities in the occurrence of the fauna of temporary pools. In these years when the pools have not got a drop of water during summer and autumn, and in which they are dried up at the beginning of the winter, are filled with snow during the winter, and get no water until the spring, the resting stages of the fauna will be hatched in spring, and the animals will then begin life under favourable stable life conditions. In years of this kind the fauna will be present with almost all its representatives. On the other hand, if the pools get water already in the autumn, freeze and thaw several times during the winter, and are then frozen over from the middle of January to April, very many of the resting stages have been developed during the periods of thaw in November—December; then when the ponds freeze to the bottom, the animals developed from the resting stages are killed, and will not be present, or will at all events be extremely rare in spring.

The above view is partly based on observations in North Seeland in 1919—20 when the ponds began the winter quite dry whereupon in the spring of 1920 we had a pronounced Phyllopod year and many of the above-named rotifers; partly on observations in the years 1910—1912, when the pools were all filled with water to ca. 1/I and when after short periods of frost before January I got larvæ of *Limnetis*, *Branchipus*, further *Triphylus*, and other rotifers, whereas during the spring I could not get a single specimen of these animals. All resting stages were hatched in November—December, and the whole material was killed when the ponds were frozen to the bottom in February—March.

The more one studies the ponds and their fauna, the more one gets the impression that it is in the first place the meteorological factors, and quite especially the temperature and the amount of rainfall, which determine the life of the plankton organisms, their nutriment, the length of their maxima and the moment when the sexual periods set in. When the temperature rises, when the concentration of the substances dissolved in the water increases, when the period is drawing near when the life of the individual is threatened, the moment arrives when the resting stages, the result of a sexual period, are formed. Specimens and generations of specimens may then die out, but by means of the resting stages the locality is preserved for the species. —

But beyond certain limits dependent on the protoplasm of the organisms and varying from species to species, variations in external conditions are unable to influence the organisms; when these are no more in harmony with the surrounding medium, this almost always causes eradication of the species in the said locality.

This is a phenomenon which is very common especially in small ponds and which contributes to convey an impression of want of stability in the composition of the fauna. —

### c. Some Remarks with Regard to the pH Values of our Ponds.

Having become acquainted with the very interesting results of HARRING and MYERS I asked my assistant Mr. KAY BERG to determine the hydrogen ion concentration in almost all the ponds used for my investigations. Already before that Mr. POULSEN had carried out the same determinations in 150 fresh waters scattered over the whole country and at present Mr. NYGAARD is following the yearly and daily variations in hydrogen ion concentration in a series of ponds near Hillerød.

The results of Mr. Kaj Berg are as follows. It is the calorimetric method of S. P. L. Sørensen which has been used: the standard values employed are as follows:

3.6 4.0 4.4 4.8 5.2 5.6 6.0 6.4 6.8 7.2 7.6 8.0 8.4 8.8 9.2 9.6.

	pH	Temp.	Date	Hour
Carls Sø .....	7.2	16.0	5/7 29	11
Branchipus Dam .....	4.7	14.9	—	11
Lille Torkeri Dam .....	6.0	17.2	—	11
Torkeri Sø .....	6.9	17.0	—	11
Pond west of the railway (Hestehaven) ..	7.5	16.5	—	12
Jægerbakke Dam .....	9.4	18.5	5/6 29	14
Slotsø .....	8.9	14.8	—	16
Spejl Dam .....	7.5	12.8	—	16
Sorte Dam .....	7.0	12.8	—	16
Badstue Dam .....	7.6	13.1	6/6 29	9
Gadevang Mose .....	6.4	12.5	—	10
Strødam: Pond in the meadow .....	7.2	12.5	—	11
Spejlet .....	8.4	13.1	—	11
Det brune Øje .....	7.6	11.1	—	11
Store Dam .....	7.6	13.8	—	11
Triphylus moor near Gadevang .....	4.8	13.5	—	13
Funke-Dam .....	7.6	16.0	—	16
Hjorte Sø (Ringkanalen) .....	6.8	19.5	—	16
Fantasi Dam .....	7.5	15.5	10/6 29	15
Fønstrup Dam .....	7.8	15.4	18/6 29	14
Grib Sø .....	4.7	19.8	—	16
Hestesko Dam .....	7.5	12.8	5/6 29	16
Sorte Dam in the Royal Gardens .....	7.0	12.8	—	16
Pond in Bøndernes Mose .....	4.4	21	—	15
Teglgaard Sø .....	7.5	18.3	22/6 29	14
Lille Grib Sø .....	5.0	22.4	18/6 29	15
Faurholm Mose, stor Grav (Nr. 1) .....	7.2	15.3	9/7 29	9
Faurholm Mose, lille Grav (Nr. 2) .....	7.1	15.0	—	9
Faurholm Mose, lille Grav (Nr. 3) .....	6.8	12.5	9/7 29	9
Esrom Sø .....	8.4	16.2	6/7 29	12
Fredensborg Slots Dam .....	7.3	18.2	—	13
Endrup Dam .....	8.5	19.8	—	13
— — pond near the road .....	6.9	17.5	—	13

	pH	Temp.	Date	Hour
Asminderød Dam .....	7.3	17.6	—	14
— Dam ved Sprøjtehus .....	7.3	18	—	14
Asminderød Dam i Krohave .....	7.4	16.2	—	14
Grønholt Dam .....	7.2	16.5	—	14
Fure Sø .....	8.4	16.2	<sup>10</sup> / <sub>7</sub> 29	10
Løg Sø .....	7.4	17.5	—	11
Ager Sø .....	8.8	17.2	—	11
Stutteri Dam .....	7.2	18.0	—	18

If we try to group the localities where pH has been measured in the well-known types: lakes 1), small pond-lakes and ponds 2); eutrophic ponds 3); temporary pools 4), moors 5) and Sphagnum moors 6), we shall arrive at the following results.

1) Lakes.

Esrom Sø .....	8.4
Fure - .....	8.4

They are both alkaline.

2) Small pond-lakes and ponds.

Ager Sø .....	8.8	Strødam: Store Dam .....	7.6
Carl Sø .....	7.2	— Det brune Øje ..	7.6
Funke Dam .....	7.6	Teglgaards Sø .....	7.5
Fantasi — .....	7.5	Torkeri Sø .....	6.9
Fønstrup Dam .....	7.8	Badstue Dam .....	7.6
Grib Sø .....	4.7	Stutteri — .....	7.2
Spejl Dam .....	7.5	Løg Sø .....	7.4
Sorte — .....	7.0		

The rule is that small pond-lakes and ponds are neutral or slightly alkaline (exceptions: Grib Sø (acid) and Ager Sø: (alkaline).

3) Eutrophic ponds.

Pond in Hestehaven .....	7.5	Ponds upon Strødam .....	8.4
Jægerbakke Dam .....	9.4	Slots Sø .....	8.9
Ponds upon Strødam .....	7.2	Hestesko Dam .....	7.5

Fredensborg Slots Dam . . .	7.3	Ponds near Asminderød . . .	7.3
Endrup Dam . . . . .	8.5	— — — . . .	7.4
Ponds near Asminderød . . .	7.3	Grønholt . . . . .	7.2

The eutrophic ponds are, therefore, alkaline, sometimes in very great degree (their pH value is, however, subject to very extensive oscillations, most probably owing to the influence of the phytoplankton).

#### 4) Temporary ponds

Branchipus pond . . . . .	4.7
Lille Torkeri pond . . . . .	6

The measured pH values are acid (since, however, temporary pools are of very different types, it is highly probable that a greater series would show great deviations).

#### 5) Fens and moors.

Gadevang moor . . . . .	6.4
Great Faurholm moor . . . . .	7.2
Faurholm moors . . . . .	7.6
— — . . . . .	6.8

These moors seem to be almost neutral, the Gadevang moor has some Sphagnum.

#### 6) Sphagnum moors.

Triphylus moor . . . . .	4.8
Pond in Bøndernes Mose . . . . .	4.4
The little Grib lake . . . . .	5
The Hjortesø . . . . .	6.8

The Sphagnum moors are highly acid.

As mentioned above, HARRING and MYERS maintain that the rotifer distribution is directly dependent upon the hydrogen ion concentration. SKADOWSKI (1923 p. 341) finds that the different groups of zooplankton, Flagellata, Sarcodina, Ciliata, Rotifers and Entomostraca, are limited to well-defined pH ranges. With regard to *Asplanchna intermedia* TAUSON (1925 p. 130, 1926 a p. 355) arrives at the result that the entire life history of *Asplanchna* is controlled by the same factor. In our country POULSEN (1928 p. 203) has tried from a large material to show



accordance between the distribution of the Entomostraca and pH; but as far as I can see without greater success. With regard to the higher plants IVERSEN (1929 p. 276) has shown in a very instructive paper that the hydrogen ion concentration directly or indirectly exerts its influence on the distribution of the water plants in Nature. —

Now with regard to the Rotifera I came to a result almost similar to that of HARRING and MYERS; only I suppose that the pH range of the individual species is not always so narrow as these authors assume.

As far as I can see, some rotifers may live in waters with very great deviations with regard to pH.

For this supposition I find support in the fact elucidated by Miss TAUSON herself, that the pH values during a summer day and night may show extreme oscillations; IVERSEN (1929 p. 326) has also noted this fact. When Miss TAUSON supposes that the animals go down into deeper water layers where the oscillations are not so great, it may be pointed out that in the main my ponds have only depths below one meter and never exceeding 3 m. That the pH values should show such great oscillations in such shallow ponds that the life of the rotifers should be more possible at the bottom than at the surface does not seem very probable. — Our explorations seem to show that the Rotifera may live in waters with very great deviations in pH. On the other hand there is no doubt that waters with a very low pH value, as the Sphagnum moors, have their quite specific rotifer fauna, consisting mainly of Notommatida.

In the tables p. 72 I have given the rotifer plancton in a) an alkaline lake: Furesø (pH 8.4) b) an alkaline pond-lake, Frederiksborg Castle Lake (pH 8.9); a neutral pond, Asminderød Pond (pH 7.3) and two acid ponds Gripsø (pH 4.7) and Klaresø near Hellebæk (4.8).

In the three first-named the investigations were carried out in the same year 1901, in Gripsø in 1909, and in Klaresø in 1923. I regret very much that for want of a boat I have been unable to carry out regular plancton investigations in Klaresø, one of our most interesting ponds, especially because it contains *Holopedium gibberum* hitherto only found in very few Danish waters. With regard to the values of pH as a factor determining the distribution of rotifers, the tables clearly show that no less than 10 rotifers are common in our most alkaline water, Furesø, and our most acid waters, Gripsø and Klaresø. These rotifers may therefore be said to be able to live at pH values from 4.8 to 8.9.

These species are the following:

*Synchaeta pectinata.*  
*Polyarthra platyptera.*  
*Rattulus capuzina.*  
*Ploesoma Hudsoni.*  
*Asplanchna priodonta.*

*Notholca longispina.*  
*Anurea cochlearis.*  
 — *aculeata.*  
 — *tecta.*  
*Conochilus volvox.*

## a) Furesø (pH 8.4).

	10/1	22/1	6/8	24/8	8/4	23/4	15/5	27/5	7/6	30/6	15/7	30/7	15/8	7/9	2/10	21/10	16/11	17/12
.. Synchrona pectinata ...	..	..	FF	FF	r	r	+	r	..	FF	..	FF	FF	..	FF	FF	..	FF
.. — tremula .....	..	..	..	..	r	..	FF	r	r	..	..	..	..	FF	..	..	FF	..
.. Polyarthra platyptera .	r	FF	r	r	r	r	FF	FF	r	FF	r	FF	FF	+	r	r	FF	r
+ Rattulus capuzinus.....	..	..	..	..	..	..	FF	r	r	FF	FF	r	r	r	r	r	FF	FF
.. — bicornis .....	..	..	..	..	..	..	..	..	..	FF	..	FF	..	FF	FF	FF	FF	FF
.. Diurella tenuior.....	..	..	..	..	..	..	..	..	..	..	FF	..	FF	FF	r	FF	r	FF
.. Gastropus stylifer .....	..	..	..	..	..	..	..	FF	FF	FF	r	r	r	FF	FF	FF	..	..
+ Ploesoma Hudsoni .....	..	..	..	..	..	..	..	FF	FF	r	r	FF	FF	r	FF	FF	..	..
○ Ascomorpha agilis.....	..	..	..	..	..	..	..	..	..	FF	r	FF	..	FF	FF	FF	..	..
+ Anapus testudo.....	..	..	..	..	..	..	..	..	..	FF	FF	FF	..	FF	FF	..	..	..
.. Asplanchna priodonta .	..	..	..	FF	FF	r	r	FF	FF	r	r	FF	FF	r	FF	r	r	r
○ Notholca striata.....	FF	r	r	r	+	+	FF	FF	..	..	..	..	..	..	..	..	..	..
○ — acuminata.....	FF	r	r	r	r	r	r	..	..	..	..	..	..	..	..	..	..	..
○ — longispina.....	..	..	..	..	FF	FF	FF	+	+	r	FF	r	FF	FF	FF	r	FF	FF
.. Anuræa cochlearis.....	FF	..	FF	..	FF	r	r	r	+	FF	FF	FF	FF	r	+	c	+	+
.. — aculeata .....	FF	..	..	FF	FF	+	c	r	r	FF	..	FF	FF	r	r	+	+	r
○ Floscularia libera .....	..	..	..	..	..	..	..	..	FF	..	FF	..	FF	FF	FF	..	..	..
.. Conochilus volvox .....	..	..	..	r	FF	FF	r	r	+	r	FF	..	..	..	FF	..	FF	..
.. Triarthra longisetata....	FF	r	r	r	r	r	r	+	+	FF	FF	FF	FF	r	r	r	FF	r
.. Pompholyx sulcata.....	..	..	..	..	..	..	..	..	..	r	r	FF	r	+	r	FF	..	..

## b) Frederiksborg Castle Lake (pH 8.9).

	1/1	15/1	1/2	15/2	1/3	15/3	1/4	15/4	1/5	15/5	1/6	15/6	30/6	15/7	1/8	15/8	1/9	15/9	1/10	15/10	1/11	15/11	1/12	15/12
.. Synchrona pectinata ...	..	..	..	..	r	FF	+	+	r	r	FF	..	..	..	+	+	+	+	r	FF	..	..	..	..
.. — tremula .....	..	..	..	..	r	FF	r	..	..	..	..	..	..	..	..	r	..	..	..	..	..	..	..	..
.. Polyarthra platyptera .	FF	FF	r	..	c	c	+	r	r	r	r	r	r	r	r	..	r	+	+	+	r	r	r	r
+ Rattulus capuzinus.....	..	..	..	..	..	..	..	..	..	FF	FF	FF	FF	FF	r	+	+	+	+	FF	FF	..	..	..
.. — bicornis .....	..	..	..	..	..	..	..	..	..	FF	..	r	..	r	..	+	..	..	..	..	..	FF	..	..
.. Gastropus stylifer.....	..	..	..	..	..	..	..	..	..	..	..	..	FF	FF	r	FF	..	..	..	..	..	..	..	..
.. Asplanchna priodonta .	..	FF	..	..	r	r	+	+	c	c	c	+	r	FF	FF	..	FF	+	+	r	r	r	FF	FF
○ — Brightwelli .....	..	..	..	..	..	r	+	+	r	+	r	..	..	..	..	..	..	..	FF	..	..	..	..	..
○ Notholca longispina ..	..	..	..	..	r	r	+	r	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
.. Anuræa cochlearis.....	..	+	+	..	+	c	cc	cc	cc	c	+	+	+	+	+	+	+	+	c	c	+	..	r	r
.. — aculeata .....	..	+	+	..	r	+	r	c	cc	+	r	+	FF	r	r	r	+	+	+	r	+	..	c	r
○§ — tecta .....	..	FF	..	..	..	..	..	..	..	FF	..	FF	..	r	..	..	..	..	..	..	..	..	..	..
○ Brachionus pala .....	FF	r	r	..	+	c	c	c	c	+	..	FF	FF	FF	r	r	r	r	+	+	..	+	r	r
○ — angularis .....	r	r	r	..	+	+	r	r	c	c	FF	FF	FF	..	FF	..	r	r	r	r	..	r	r	r
§ — urceolaris.....	..	..	..	..	..	..	..	..	..	FF	..	..	..	..	..	..	..	..	..	..	..	..	..	..
.. Conochilus volvox .....	..	..	..	..	..	..	..	r	r	FF	..	..	..	..	..	..	..	..	..	..	..	..	..	..
○ Conochiloides natans..	..	..	..	..	..	..	..	..	..	r	FF	..	..	..	..	..	..	..	..	..	..	..	..	..
.. Triarthra longisetata....	r	..	r	..	r	r	+	c	r	r	+	+	r	..	..	..	+	+	+	..	..	..	r	r
.. Pompholyx sulcata.....	..	..	..	..	..	..	..	..	..	r	+	c	c	+	+	c	+	+	r	r	..	..	..	..

## c) A small pond in North Seeland without vegetation (pH 7.3).

	12/8	30/8	4/4	21/4	1/5	15/5	1/6	14/6	28/6	8/7	15/7	1/8	15/8	30/8	14/9	1/10	15/10	1/11	15/11	2/12	15/12	
.. Synchaeta pectinata .....	rr	cc	c	r	r	rr	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
.. — tremula .....	rr	cc	c	r	rr	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
.. Polyarthra platyptera .....	rr	c	cc	cc	c	+	r	rr	..	..	..	r	r	rr	..	r	r	..	c	c	c	c
§ Anarthra aptera .....	..	..	r	c	+	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
§ Rattulus cylindricus .....	..	..	..	..	..	..	..	..	..	rr	r	r	r	r	r	r	r	..	..	..	..	..
.. — bicornis .....	..	..	..	..	..	r	rr	r	r	r	r	r	r	r	rr	r	..	..	..	..	..	..
.. Diurella tenuior .....	..	..	..	..	..	r	rr	r	r	..	rr	..	r	..	..	..	rr	..	..	..	..	..
§ Notops hyptopus .....	..	..	r	+	c	+	r	rr	rr	..	..	..	..	..	..	..	..	..	..	..	..	..
.. Gastropus stylifer .....	..	..	..	r	r	r	rr	..	rr	..	..	..	..	..	..	..	..	..	..	..	..	..
○ Asplanchna Brightwelli ..	..	..	..	..	r	r	c	c	+	..	r	rr	..	..	rr	r	rr	..	r	..	..	..
○ Ascomorpha agilis .....	..	r	r	r	+	cc	c	rr	..	..	..	..	..	..	..	..	..	..	r	rr	r	r
§ Rhinops vitrea .....	..	r	+	cc	cc	cc	rr	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
.. Anuræa cochlearis .....	r	rr	rr	c	cc	cc	cc	cc	c	c	c	c	c	c	c	cc	ccc	c	cc	cc	c	c
.. — aculeata .....	..	c	c	cc	cc	cc	cc	c	r	r	rr	r	r	r	r	+	+	c	c	c	c	c
○ § — tecta .....	..	..	..	..	..	cc	cc	cc	+	r	r	+	r	+	c	cc	cc	c	cc	c	c	c
§ — hypelasma .....	..	..	..	..	..	..	..	..	..	..	+	c	c	+	r	rr	rr	..	..	..	..	..
○ Brachionus pala .....	..	..	..	+	c	c	cc	r	r	rr	r	..	rr	r	..	rr	r	..	r	r	r	+
○ — angularis .....	rr	r	r	r	r	+	c	c	cc	+	+	r	..	rr	r	rr	r	r	r	r	r	+
§ — urceolaris .....	..	..	..	..	..	..	rr	..	rr	..	..	..	rr	..	..	..	r	..	..	rr	..	..
§ — Bakeri .....	..	..	..	..	..	..	rr	..	rr	..	rr	..	rr	..	rr	..	..	..	..	..	..	..
○ § Schizocerca diversicornis ..	..	..	..	..	..	..	rr	+	c	c	c	c	+	rr	rr	..	..	..	..	..	..	..
.. Triarthra longisetata .....	r	+	+	c	c	cc	c	r	+	+	c	cc	c	+	r	+	c	+	c	r	c	c
§ — breviseta .....	..	..	..	..	r	+	rr	+	r	..	..	..	..	..	..	..	..	..	..	..	..	..
.. Pompholyx sulcata .....	..	..	..	..	..	..	..	..	..	..	r	r	+	c	cc	+	rr	..	..	..	..	..
§ — complanata .....	..	..	..	..	..	..	..	..	..	..	rr	rr	r	..	..	..	..	..	..	..	..	..
○ § Pedalion mirum .....	..	..	..	..	..	..	..	..	..	..	r	+	c	c	r	rr	..	..	..	..	..	..

## Gripsø (pH 4.7).

	26/8	20/4	2/5	24/5	5/6	21/6	9/7	26/7	5/8	17/8	16/9	29/9	17/10	8/12
.. Synchaeta pectinata .....	..	..	rr	rr	r	..	..	..	..	..	..	r	r	r
.. Polyarthra platyptera .....	..	r	ccc	ccc	+	+	r	..	r	r	..	..	..	+
.. Asplanchna priodonta .....	..	..	r	..	..	..	..	r	rr	rr	rr	..	..	..
.. Anuræa cochlearis .....	rr	rr	rr	..	rr	..	rr	r	rr	..	..	..	..	w
.. — aculeata .....	..	..	..	..	rr	rr	..	..	rr	..	..	..	..	w
§ — sevrulata .....	rr	..	rr	..	..	..	..	..	..	..	..	..	..	..
.. Conochilus volvox .....	..	..	..	..	..	..	..	..	..	rr	rr	..	..	..

## Klaresø (pH 4.8).

	23/5	20/6	21/7	7/8	20/8	6/9	14/9	15/10
.. <i>Polyarthra platyptera</i> .....	+	r	r	r	c	+	r	r
+ <i>Rattulus capuzina</i> .....	rr	+	+	c	+	rr	..	..
○§ — <i>longiseta</i> .....	..	rr	cc	rr	..	..	..	..
.. <i>Ploesoma Hudsoni</i> .....	..	..	rr	+	+	rr	..	..
.. <i>Asplanchna priodonta</i> .....	..	..	+	r	r	rr	rr	..
○ <i>Notholca longispina</i> .....	ccc	rr	..	..	..	..	..	..
.. <i>Anuraea cochlearis</i> .....	r	r	+	+	c	+	r	r
.. — <i>aculeata</i> .....	..	..	rr	rr	..	..	..	..
○§ — <i>tecta</i> .....	..	..	..	rr	..	..	..	..

The tables illustrate rotifer life the whole year round in a) a lake; b) a small highly eutrophic lake; c) a small eutrophic pond; d) two oligotrophic ponds.

.. ubiquitous; + mainly species belonging to larger lakes; ○ mainly forms belonging to small ones; § mainly forms from small ponds.

rr very rare; r rare; + rather common; c common; cc very common; ccc abundant.

Samples taken in ponds with very brown peaty water, but whose pH value has not been determined, very often contain *Ascomorpha agilis*, *Synchaeta tremula* and *Gastropus stylifer*. Further investigations will most probably range these species in the same category. —

As far as I can see, these results do not seem to corroborate the view of HARRING and MYERS that the distribution of rotifers is directly dependent on the hydrogen ion concentration. This may perhaps hold good for certain species, but not for all.

The list shows the peculiar fact that *Brachionus* is totally wanting in ponds with very low pH values; it is questionable whether this is due to the acidity of the water since they are also absent or at all event extremely rare in the large highly alkaline lakes. Their home seems in the first place to be eutrophic ponds, with pH oscillating round the neutral point.

In Gripsø rotifer life shows the great peculiarity that it is almost totally restricted to spring and that only one single form *Polyarthra platyptera* has a large maximum at that season. From June to December it is only with the greatest difficulty that I have found a few rotifers in the samples. At that time the zooplankton is almost entirely formed of *Diaptomus* and *Ceriodaphnia quadrangula* var., *hamata*; the phytoplankton of *Peridinium Willei*, *Dinobryum*, *Ceratium hirundinella* and *Mallomonas*. The phenomenon relating to the periodicity of the rotifers is the same year after year; it seems, furthermore, that only *Polyarthra* gets a great maximum. Why the Rotifera totally disappear from June to December, and why the summer rotifers are not represented by a single species, I do not know. That this should be caused by yearly variations in pH is highly improbable, especially

because variations in pH during the summer months would most probably show higher values.

If we only consider Gripsø we might be inclined to suppose that the extremely low pH value had caused the scarcity of rotifers; that this cannot be the case however will be understood when we consider the plancton of Klaresø. Here we shall find large maxima, and the pronounced summer-forms are well represented. pH in the two lakes is almost the same.

With regard to the tables (p. 72—74) the following remarks should be added.

The tables further show that the rotifer plancton of larger lakes consists mainly of ubiquitous; they are, furthermore, mainly identical with those of smaller lakes; of species only belonging to the pelagic region of larger lakes there are very few. In the lakes most of the plancton rotifers get only relatively small and modest maxima. Sexual periods are difficult to detect and really often seem to be wanting.

The rotifer life of smaller lakes does not differ very much from that of the ponds. Most of the ubiquitous have large or very large maxima in small lakes and in ponds; most probably they are often acyclic in lakes, monocyclic or dicyclic in small ponds; in many ponds they may be polycyclic, perhaps mainly in more southern latitudes. A maximum almost always precedes a sexual period. The period of greatest propagation for the ubiquitous is almost always in spring. The tables further show that some rotifers are pronouncedly perennial, some are periodic and closely associated with quite definite periods of the year (e. g. *Gastropus stylifer*, *Ploesoma Hudsoni*, *Anuraea hypelasma*, *Pompholyx sulcata*, *Pedalion mirum* are all pronounced summer forms. *Rhinops vitrea* is a pronounced spring form). —

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## Chapter V.

### The Periodicity of the Rotifera and related Problems.

#### **Notommatidæ.**

Hitherto no one has been able to give a more detailed description based on studies in Nature of the cyclic propagation of one of the species of the great family *Notommatidæ* in a free-living stage.

This is partly due to the great systematic difficulties, partly to the fact that great maxima have only rarely been observed in Nature. When studying the more primitive, mainly creeping, rotifers e. g. these very *Notommatidæ*, the observer is compelled to assume that many of these species are present in the ponds almost the whole year round and over long periods almost in the same number. Commonly there is a slight maximum for many of these species in spring, but it is not

strongly marked; it seems as if maxima may also occur in summer, and as late as December many of the species may still be rather numerous. The males are only very rarely seen, always in single individuals and as far as I know never in the "waves" known from many other families. Many observers have most probably had the same supposition that sexual reproduction had almost ceased and only took place now and then and at great intervals. Experimental work carried out in the laboratory only confirms this view (*Proales*).

As mentioned in my Contributions pars I (1923, p. 201) many of our smallest ponds are covered with a green scum, algæ-carpets, in some ponds consisting of *Euglena*, in others of other Flagellata, of *Spirogyra*, or other algæ; in some carpets *Lemna* were interwoven with *Spirogyra* threads, in others watermosses covered most of the surface. Now when this surface was skimmed of *Euglena* and other Algæ and put apart in a vessel, it was seen that this very carpet was covered with innumerable rotifers. In the different ponds the number of species was not great, but a single species could be present in very many specimens. If then a glassplate was taken and cautiously put below the green surface coating, and the material then put in a white porcelain vessel, it could be brought home and easily studied under the binocular aquarium microscope. In this way it was shown that many rotifers, especially those belonging to the *Notommatidæ*, but also many others with them, lived a half swimming, half creeping, life on the lower surface of these algæ coatings. Especially upon sunny days there were very few in the waterlayers below. Just in these coverings, they easily find their food; but perhaps first of all they find those high temperatures which are necessary for the ripening of the eggs. On sunny days in spring the temperature in the algæ coverings may rise to about 28° C., whereas in waterlayers only a few inches below the surface it does not reach 20° C.; it may be added that in early frosty nights these carpets may be covered with a thin layer of ice. It often happened that an alga carpet from a single little pond only contained one single species, in that case occurring in countless numbers. If then, at intervals of only a few days, pieces of the carpet with animals and eggs were brought home to the laboratory, an insight into the course of the maximum could be gained. In this way males used for the description (part I) were, in fact, found, but in very many cases it was shown that the maxima are not followed by distinct sexual periods, and that they are mainly formed by amictic females. In many cases it could be shown that heavy showers, diluting the water and lowering the temperature from about 24° C. to 12—14, might suddenly kill the whole colony; furthermore, that suddenly appearing very high temperatures, 28—30° C., had quite the same influence. In these cases it was supposed that the extreme temperatures prevented the development of a sexual period. On the other hand in very many cases it seemed that the maxima were finished without any sexual period and without any possibility of ascribing this result to external conditions. To take colonies of this kind into the laboratory and try to produce sexual periods was always a waste of time. On the other hand, if colonies were taken

which were in the middle of their sexual period, this was often continued in the vessels and males and resting-eggs appeared. This was the case with species of the genus *Diglena* with *Copeus caudatus*, *C. pachyurus*, *Notommata najas*, *N. aurita*, different species of *Proales* etc. It must, however, be emphasized that the sexual period always seems to be extremely short, and that it is a mere chance if you just happen to hit upon it.

In the last part of June, after a series of days with bright sunshine and hot weather, the water in many of the ponds and the small holes in the peat bogs often sinks very much. The temperatures in the algæ coverings rise almost to 30° C. On exploring them now, it is seen that only very few rotifers are present, but on threads etc. different resting-eggs are found, as far as I could see, however, in a relatively small number. — In the very wet summer of 1922 the ponds and holes often got water again already in July; the algæ coverings appeared again over the surface, but nevertheless the abundant rotifer life from May did not reappear. — None of the species were now present in countless numbers, many had quite disappeared, most of them were present in a very few specimens. The coverings were visited the whole summer and autumn; the result of the exploration was always the same; no maxima and no sexual periods appeared. It is possible that this was only due to the very cold rainy weather and the very few bright sunny days in the last part of summer and autumn. This supposition is corroborated by the fact that in other years, in the holes in a peat bog covered with algæ, I found several *Notommatidæ* with large maxima in September.

The great difficulty in these studies carried on in Nature is that maxima and sexual periods are found accidentally and often too late. Then when the very same locality is studied at the same time the next year, none of these rotifers are found.

However fugitive these studies of the periodicity and sexual periods of the *Notommatidæ*, are most of them seem to strengthen the supposition that the fairly frequent great maxima in many species are not followed by sexual periods of such a distinctness and significance as among pelagic rotifers. In many localities and in many years sexual periods may be totally suppressed, the whole development belonging to amictic females. If this is correct, this fact may probably be connected with another fact, namely that just these rather primitive rotifers may be able to endure drought periods of considerable length as well as rather low temperatures. Only very few of these species have been studied in cultures in the laboratory; but the results of the studies agree with the above-named supposition. The investigations of NOYES (1922 p. 237) on *Proales decipiens* show that "neither a change in the kind nor the concentration of the culture medium, a constant or fluctuating change in the temperature, or a change in the chemical constitution of the medium has been accompanied by the appearance of the male in *Proales decipiens*." The cultures have shown continuous parthenogenesis for about 25 generations. As, however, it has been stated that during the first but not the second winter two sorts of eggs, thin-shelled and thick-shelled eggs have appeared, it may have been pos-

sible that males might have been present, and that the thick-shelled eggs are deposited by a mictic female (p. 235).

With regard to another species, *Proales sordida* Gosse, JENNINGS and LYNCH (1928 p. 348) also maintain that in their long-continued cultures, often under conditions that induce the appearance of males in certain other species, males have never been seen. Reproduction seems to be exclusively parthenogenetic. —

On the other hand, it must be remembered that in the parasitic species of the same genus, *P. wernecki* in *Oedogonium*-threads and *P. parasita* in *Volvox*, males are well known. Among *P. wernecki* they have been found by ROTHERT (1896 p. 702) and by ROUSSELET (1897 a p. 415) among *Proales parasita* in *Uroglena* by myself (1923 p. 221) and by ZAWADOWSKY (1916 p. 287). Furthermore PLATE has also found males among *Hertwigia volvocicola* (1886 p. 27) nearly related to *Proales*. The peculiar fact that we are always able to find males in those cases where, owing to the limited space in which they live, it would be almost an impossibility for them to escape the observer, would seem to suggest great caution with regard to conclusions.

The colonies of these algæ are rather short-lived, their maxima may be great, and when they are at an end, they totally disappear from the watermasses; this especially holds good with regard to *Uroglena*. It is a well known fact that the rotifers may exist and in reality do exist independently of the algæ; it seems as if the amictic females seek the algæ, force their way through the cell walls, and through their gelatinous coatings. Here, in the algæ, the mictic females appear to give rise to male eggs, males, and later on resting-eggs. It would seem, therefore, that the two sorts of females among these parasitic rotifers have a very different life, the one mainly free-living, the other perhaps almost exclusively parasitic. — A more thorough study of these rotifers living in pelagic algæ would be extremely desirable.

All in all it seems that among the *Notommatidæ* the mictic females play a very slight rôle. Lacking in great parts of this area of distribution, they may often be totally absent and only appear now and then and under quite special hitherto little known life conditions. It further seems that the above-named algæ carpets especially on bright sunny days with temperatures about 25° C. and especially in May are able to develop just those conditions which cause the appearance of mictic females.

### ***Triphylus lacustris* (Ehrbg.).**

Plate XIV, fig. 3—5.

In a turf-pit which never contained more than some litres of water, *Triphylus lacustris* was present in the beginning of May 1928 but only in few numbers. In the middle of May and in the first part of June it was very common. Being anxious to study the males when they appeared, I visited the hole every week. By 2/VI the hole contained numerous *Triphylus* but, as far as I could see, only amictic females. Eight days later I only saw females with large yellow resting-eggs, which



were later on deposited in my vessels. Then the species disappeared and it was not observed later on in the year.

In 1929 we had still frost during the night by 1/V. All pit-holes were covered with ice. By 8/V *Triphylus* was found in the same pithole as in 1928. Twenty-five specimens were isolated, but the culture died out in the course of a few days. During the period 8/V to 10/VI the pithole was visited eight times. It seems impossible to keep the animals alive in cultures; they invariably died. In nature the animal has no real maximum; in the large samples about 20—25 specimens may be found. Till 30/V only amictic females were observed. At that time a very few males were seen and simultaneously a few females with resting-eggs. These were found again on 6/VI; then the pit-hole began to dry up and by 15/VI, when the hole was reduced to moist sphagnum, no specimens were found. Later on the hole was again filled with water, but *Triphylus* was not found the rest of the year.

### **Notommata sp.**

Plate II, fig. 1—5.

In Fjenneslev Pond in the middle of Seeland, a pond which has often been explored during the last 10 years, a peculiar rotifer was found in August 1929. It is the same pond in which *Asplanchna Sieboldi* has been studied, and in which my assistant Mr. Berg found *Daphnia Atkinsoni*, and *Moina rectirostris*, both common in the pond. The pond also contained *D. magna*. On examining the *Daphnia* found on 15/VIII 1929, I saw to my great astonishment that a good deal of the specimens carried an extremely hyaline, rather large rotifer, which was either fastened to the carapace or crept slowly over its surface. The *Daphnia* would sometimes carry two or three specimens, commonly only one. It was about 500  $\mu$  large. The animal was extremely variable in form; annulations were not very conspicuous; it had a well-marked foot, terminating in two strong toes; the foot could almost be wholly withdrawn into the body and stretched out to a length of more than  $\frac{1}{3}$  of the whole body. The wheel organ was mainly a cilia-covered disc, the cilia at the borders of the disc not very prominent; the disc was placed rather ventrally. The mastax was globular, rather small, the mouth-parts somewhat irregular, but presumably mainly of the malleate type, the incus and especially the rami were fairly well developed. A rough sketch is given. The large stomach carried two globular gastral glands; these glands differ in size and form in different specimens. They are often furnished with a tip to which a very little muscle is fastened; in some cases I saw that they contained two very large globules; the ovarium was large, globular, and somewhat lobate, with eight nuclei; there was a contractile vesicle and the nephridia bore at all events four vibratile tags. Peculiar were the extremely large food glands, terminating in a heart-shaped reservoir with thick walls. On the underside of the brain an inconspicuous eye was observed. In some specimens no eye could be observed. There is a dorsal organ to which two nerves are running. —

Two lateral organs were found lying near the beginning of the foot and connected with the brain by means of two nerves. The muscle system was very well developed. On a dorsal view the cuticle was seen to possess some longitudinal furrows or stripes which were fairly constant. —

When visiting the pond in May 1930 I found the Daphnids of the pond covered with coatings of green algæ. Many specimens of *Brachionus urceolaris* var. *rubens* were fastened to the valves; furthermore the *Notommata* were found again, but now they were much rarer. Whereas the *Brachionus* were numerous as free-swimming organisms the *Notommata* were only found on the carapaces of the Daphnids. When detached by force, they swam very slowly; auricles were never observed. Only amictic females either without or with a very large egg were seen. — Before 15/VIII 1929 the pond had not been visited for a month and when I next visited the pond on 26/VIII not a single specimen was to be found on the *Daphnia*.

It might be supposed that the animals would deposit their eggs on the shells of the Daphnias. For a long time I searched in vain, but at last an egg was found agglutinated dorsally to the head shield and just above the root of the second pair of antennæ, a little in front of the heart. It was then seen that in twenty-one cases eggs were found, and always in a number of one or two, agglutinated to this part of the shield. The place is admirably chosen. It is almost the only part of the carapace where the second part of the antennæ are unable, during their movements, to sweep off the eggs. Because of the thick jelly and strong threads given off from the enormous footglands the animals themselves cannot be swept off by the rami. On the other hand, it is most probably impossible to fasten the eggs on the valves over which the feathered bristles of the antennæ are constantly sweeping. They are only safe in the above-mentioned place.

As is generally known, various rotifers, especially belonging to the order *Bdelloida*, but also some *Notommatidæ* and *Pterodinidæ*, are found as ectoparasites or more probably as commensalists on different fresh-water animals (*Ostracoda Malacostraca*, shells of *Molluscs*, *Insecta*). Among these forms the one here described may also be classed. It is to be hoped that it may soon be found again and more exactly described than I, owing to want of material, have been able to do.

#### **Notommata** sp.

Plate II, fig. 6.

None of the *Notommatidæ* have hitherto been observed in the plancton of ponds or lakes. In one of the experimental ponds a peculiar rotifer suddenly appeared in August 1929, whose systematic position I am unable to determine. The skin was rather soft, but had no annulations; the foot was placed ventrally; it was very short and had two minute toes. First I regarded it as a very primitive species of *Gastropus*, most nearly related to *G. minor* but with affinities to the *Notommatidæ*. When pressed under a cover it got a form which caused it greatly to

resemble in habit those representatives of the *Notommatidæ* which live in *Uroglena* and *Volvox* and the description of which is still very deficient. There is no antenna but a very small eye. The mastax is very large, globular, containing irregular mouth-parts, mainly of the virgate type.

Almost all the observed specimens contained one single very large egg; of the vitellarium only small parts were observed. The egg was undoubtedly a resting egg. The pond had been under observation for years, but never before had the animal been observed. It was rather common in a single sample in August by 24/VIII, but already in the next month on 6/IX it had totally disappeared; later on it has never been observed. Its occurrence in the pelagic region as a free-swimming organism is an example of the phenomenon characteristic of a fairly large number of bottom organisms. During the sexual period they may live a pelagic life for a very short time or more correctly expressed: the mictic females may be free-living organisms in the central parts of ponds and lakes, whereas the amictic ones are true bottom organisms. The pond had never contained *Volvox*, and at the time when the rotifer appeared, no *Uroglena*. —

#### Synchætadæ.

According to ROUSSELET (1902 p. 270) the genus *Synchæta* comprises seven fresh-water species. *S. pectinata* Ehrbg.; *tremula* Ehrbg.; *oblonga* Ehrbg.; *grandis* Zach.; *stylata* Wierz.; *longipes* Gosse and *kitina* Rouss. I regard the species *longipes* Gosse and *kitina* Rouss. as very doubtful, at all events they may be nearly related to *tremula*.

*S. grandis* seems to belong to the pelagic region of larger lakes where ZACHARIAS (Ploener-see) first found it; later on it was found by ROUSSELET in the large reservoirs of the East London Waterworks Company at Tottenham (1902 p. 288). Whereas *S. pectinata*, which may be regarded as most closely allied to it, has often been found in our larger lakes, I have never found a form which could be related to *S. grandis*.

With regard to the eggs of the *Synchæta* ROUSSELET (1902 p. 272) maintains that the marine species carry their eggs attached to the toes till hatched, whereas those of *S. pectinata*, *tremula*, *oblonga* and *stylata* are laid in the water; those of *stylata*, being furnished with long bristles, are said to be pelagic; the eggs of the other species fall to the bottom or, owing to their somewhat sticky surface, adhere to plants etc; only *oblonga* is supposed now and then for a short time to carry its eggs, usually one, rarely two. On the other hand ZACHARIAS (vide ROUSSELET (1902 p. 273)) maintains that in the lakes of the north of Germany the two main forms *S. pectinata* and *tremula* habitually carry their eggs attached to their toes. ROUSSELET denies that this is the case in England. *S. grandis* is said by ZACHARIAS (1893 p. 35) to deposit its eggs in batches of 2—3 and these batches are said to be pelagic. All hitherto observed eggs are said to be summer eggs, only LAUTERBORN (1893 p. 12) has seen resting-eggs (*S. pectinata*); they are said to be covered with long bristles. We shall return later on to the eggs of the *Synchæta* species; here

we will restrict ourselves to the short remark that, in the *Synchæta* species, because they commonly do not carry their eggs, we are unable to distinguish mictic from amictic females.

### ***Synchæta pectinata* Ehrbg.**

Plate XI, fig. 4—6.

Frederiksborg Castle Lake. *S. pectinata* is most probably perennial, but the number of specimens is but small in most of the samples; it is most common at rather low temperatures; it always occurs before the lakes freeze; it is found below the ice, but rather rarely, and begins its maximum shortly after the ice has disappeared. The maximum lies especially in April, after which the species is rather rare all the year round. In 1898 I had the good luck to come upon a sexual period, in which males were present. There is no doubt that mictic females appear in the last part of the maximum, but it seems that their life is very short, and that it requires good luck to get them.

Asminderød Pond. *S. pectinata* is, just like *S. tremula*, a pronounced spring form, with its maximum a little later than that of *S. tremula*, commonly two to three weeks after the ice has disappeared. It was large in 1922, traceable in 1923, but very inconspicuous in 1924 after the severe winter; males were found in 1922. The species disappears totally in the middle of May, and reappears in a few specimens in December.

Fredensborg Pond. The species is only found in a few samples in spring and autumn.

Island Pond (Ødam). *S. pectinata* seems every year to have a pronounced spring maximum, during which a few males have been observed. Then it commonly disappears totally during the summer, but in contradistinction to *S. tremula* appears in September—October; in 1924 it had a rather large maximum in October.

Horseshoe Pond Hesteskodam. *S. pectinata* appears in November and, during winter, is one of the main forms below the ice. Then it gets its spring maximum, which was extremely large on 16/V 1924. During that period males and resting-eggs were found; these occurred lying free in the sample. During May—November the species seems practically to be absent.

Nøddebo Pond. *S. pectinata* is most probably perennial in some years. This was the case e. g. in 1922 and 1924. In 1923 it was only very rarely observed. In 1922 and 1924 it had very large maxima in May and June. On 10/V 1924 numerous resting-eggs were found; these eggs were found within the animal as well as free in the sample.

Funke Pond. *S. pectinata* is perennial. It has a pronounced spring maximum in April and in the first part of May; it may, as in 1910 and in 1924, be extremely large. In some years, as in 1909, the species begins to be common already in the last part of October and in the beginning of November. Again in 1929, in April, the maximum was very large.

In the other ponds *S. pectinata* has always been observed, it has always been most common in spring, now and then also in September—October. In one of my experimental ponds it was very common in July—August, and in this last-named month eggs were found floating free in the water. —

As a plancton organism in our larger lakes *S. pectinata* has been continually observed; here it seems to be present at all seasons of the year, but it is always rather rare; commonest in May—June at a temperature of 13—16° C.; males have never been observed here.

### *Synchæta tremula* Ehrbg.

Frederiksborg Castle Lake. *S. tremula* is a pronounced winter and early spring form. Commonly it does not appear before the lake freezes, but during the whole winter it is always present below the ice. The resting egg may be hatched at very low temperatures, about 0. Together with *Brachionus angularis*, *Polyarthra platyptera* and *Triarthra longiseta* it formed the winter plancton below the ice. There is a maximum immediately after the ice has disappeared; a sexual period has not been observed, however. Every year the species seems totally to disappear during the last part of April and from May to December, it is only found now and then and always in very few specimens.

Asminderød Pond. The species is a pronounced spring form. In 1922 it had a very large maximum on 31/III, but already in April it was very rare and was not observed the rest of the year. During 1923 and 1924 it was only seen in some spring samples and always only in a few individuals.

Island Pond. *S. tremula* has most probably every year a very early maximum commonly in the last part of March and early part of April. As the maximum is so short, it will not always be coincident with the taking of the samples. This was, however, the case in 1924 when it was found remarkably late, on 16/V. During the rest of the year it almost always seems to be totally absent.

Nøddebo Pond. Especially in 1922 and 1924 *S. tremula* had well-marked and very distinctly delimited maxima, always occurring in May and the first part of June, a little later than in other ponds. The resting-eggs have been found in May. Beyond this time the species totally disappears from the water. In the other regularly explored ponds we arrive at quite the same results, a pronounced, often very conspicuous, and often very short maximum always occurring in the spring, and commonly shortly after the ice has disappeared; otherwise it only appears in very small number or is totally absent.

During my numerous excursions to smaller ponds scattered over the whole country, *S. tremula* has always been found in early spring, often in enormous numbers; now and then large maxima have also been observed during summer, and this has especially been the case in very small bog-holes with brown water; here the species was often almost yellowish, and the stomach almost black; I have often seen just these specimens carry their eggs, a single large summer egg. — Now

and then autumnal maxima may also occur, especially in very small ponds but sexual periods have hitherto only been observed during spring.

It does not belong to the pelagic region of larger lakes. Single specimens may now and then be observed in samples, and especially during the spring; most probably these are individuals which are carried out into the centre of the lake by the wind or by currents.

### ***S. stylata* Wierzejski.**

Plate XI, fig. 2—3.

The well-marked species *S. stylata* is especially characterized by its long and styliform foot; furthermore by its egg which is spherical and covered with very long and thin spines; it floats in the water. I have several times, in smaller lakes in which regular explorations were not carried out, found pelagic eggs with just the appearance figured by WIERZEJSKI (1892) and ROUSSELET (1902 Pl. 4 fig. 4 a) and of just that size. I therefore suppose that this species may be commoner in our country than my explorations seem to show.

In a little pond in the Strødam Reservation in the first days of July a *Synchæta* was found, very similar to *S. stylata*. As I have been a little doubtful with regard to the determination of the species I have added a drawing. No eggs were found in the water, but many of the females contained eggs which, however, had no spines.

### ***Synchæta oblonga* Ehrenberg.**

In very small ponds which often dry out during the summer, especially in duck-ponds or in those with very dirty water, I have often found a very small *Synchæta* only about 200  $\mu$  and often somewhat smaller. It was the species which I have named *S. pectinata forma minor* in earlier publications. ROUSSELET (1902 p. 276) pointed out that this form may be Ehrenberg's *S. oblonga*, and I suppose that this may be correct.

In the above-named localities, in early spring, this little species may occur in enormous masses. The water may teem with them, so that it almost gets a milky appearance. It is a pronounced spring form, which totally disappears before May; later on in the year I have hardly ever met with it. It carries its eggs, at all events much longer than the other species. Curiously enough I have never been fortunate enough to see a sexual period. It seems as if the species, in all the localities which I know, only lives an active life for about 4—6 weeks, living the rest of the year as resting-eggs at the bottom of the water. —

1. With regard to the four species of *Synchæta* now studied it may be pointed out that *S. oblonga* belongs to the smallest ponds which often dry out during the summer; *S. tremula* to small ponds and lakes, partly with peaty water, and partly to ponds rich in organic matter. It often occurs together with *S. pectinata*, but this is also an inhabitant of larger ponds and may be found in the pelagic region of larger lakes.

2. *S. oblonga* seems to be a pronounced spring form, hitherto only found in Denmark in April—May. *S. tremula* may be perennial, but is rare after May and the same is the case in many localities with *S. pectinata*, which is on the whole the most perennial of the four species. *S. stylata* seems to be a rare species in our country.

3. All the four species may as a rule mainly be designated as pronounced spring forms with their maxima in April—May; that of *S. tremula* 2—3 weeks before that of *S. pectinata*, but often for a short time coinciding with it; autumn maxima have been observed several times.

4. Because males and resting-eggs have only been found in April—May, it is highly probable that the mictic females only occur during a very short period; the specimens occurring at other seasons of the year are all amictic ones. —

5. As stated above, I have seen *S. oblonga* carry its summer-eggs, but most probably not till they are hatched. During the great maximum in May 1924 in Funke Pond I had enormous amounts of *S. pectinata* and *S. tremula* in my vessels. Simultaneously a great maximum of *Asterionella* occurred; the diatoms sank to the bottom, and on that bottom layer the *Synchaeta* dropped their eggs; they were found there in thousands; a specimen would carry its egg a few seconds or minutes, but then it was dropped off; the *Asterionella* layer was covered by a gelatinous layer deriving from the *Synchaeta*, and the eggs were agglutinated to that. All three sorts of eggs were found (Pl. XI, fig. 4—6). During the huge *Synchaeta* maxima enormous amounts of *Synchaeta* eggs may drop downwards. Because the summer eggs, especially those of *S. pectinata*, contain oil, it may be possible that the eggs, during the short time till they are hatched, especially in not too shallow waters, may be floating in the water. The oil is not present as one single large oil globule but as minute globules gathered in irregular masses sharply defined and lying directly below the shell; the oil is reddish. The resting-eggs are dark and covered with short spines; they are found partly in the females and partly lying on the *Asterionella* layers. — Male eggs were only found in relatively small numbers.

6. The peculiar phenomenon that the two *Synchaeta* species *S. pectinata* and *S. tremula* are both perennial in most places and everywhere have large maxima in spring, commonly followed by a sexual period, which has almost only been observed in May, seems to indicate that the mictic females arrive at a rather well-marked distance from the generation hatched from the resting egg.

7. ROUSSELET (1902 p. 271) has observed that the muscles of the mastax can expand the cavity suddenly; he therefore supposes that by a sucking action the food particles, consisting of diatoms, algæ, infusoria and small rotifers, are forced into the mouth, when they are at once seized by the unci; the unci themselves are not able to be projected through the mouth; the organisms are sucked into the mouth, and then seized by the unci. This is most probably correct. I have never seen the unci come out of the mouth-opening and seize another organism; on the other hand I have very often seen a *Peridinium* lying between the unci in

the interior of the animal. The sucking action may be of greater significance for *S. pectinata* than for *S. tremula*.

Only in the peculiar *S. stylata* from Strødam have I seen the mouth-parts in the mouth-opening. When it seized a *Peridinium*, I saw the animal become much elongated; the coronal disc was then directed straight forward, the whole animal was almost cylindrical; in the centre of the disc a short tube appeared, and the mouth-parts appeared in the opening; the manubria and unci presented themselves almost as a line, and the strong rami moved against each other. I tried to take a camera sketch of the animal at that moment but it was not good enough for publication. Tab. II, fig. 7 shows a camera sketch with the mouth tube protruded.

### ***Polyarthra platyptera* Ehrbg.**

Plate XI, fig. 7—9.

Frederiksborg Castle Lake *P. platyptera* is most probably perennial; on the other hand it may be pointed out that during July—December it has only been observed singly and often only in a few samples; it appears again regularly in December and, whether or not the lake is ice-covered, during the whole winter it is one of the main forms of the rotifer-plancton; the maximum begins to develop already below the ice, and the mictic females appear in April at a temperature of 6—8° C., only about 14 days after the ice has disappeared. The mictic females then carry clusters of male eggs, often about 20. They may still be found by 15/V at a temperature of 16° C. From the middle of May, and in some years already in April, the mictic females carry the large almost black resting egg, which seems to be carried for a very long time. In the latter part of May the eggs are often found free in the water; they are, however, not pelagic and soon sink to the bottom. After the sexual period the species almost totally disappears. *Var. euryptera* has not been found in the lake.

Asminderød Pond. *P. platyptera* is most probably perennial, but during long periods the species seems to be very rare. Maxima followed by sexual periods may occur quite irregularly almost at all seasons of the year; in 1922, in April and December; in 1923, during the whole spring and then again in September; in 1924, not until December. It seems as if the species has a rather pronounced summer minimum, very conspicuous in 1922, when it was not found from 1/VI to 18/XI; the same was almost the case in 1923; in 1924 it was more common; the maxima are always followed by sexual periods.

Fredensborg Pond. *P. platyptera* was rather common during the spring of 1922 and then had a conspicuous sexual period; it had another large maximum in June; later on it totally disappeared and during 1923 was always rare.

Island Pond. *P. platyptera* occurs year after year in the two forms *forma typica* and *forma euryptera*. The typical form has its maximum at very low temperatures; mictic females with male and resting-eggs appear in the latter part of April and in May. Then the form almost totally disappears, and rather suddenly in the last part of



June forma *euryptera* appears; its maximum lies in August, but I have never succeeded in seeing this form carry males or resting-eggs; it disappears in the middle of September. Simultaneously there appears a remarkable resting egg, lying in all autumn samples. It may hypothetically be referred to this form. In November—December the typical form appears again. —

Horseshoe Pond. Curiously enough it seems as if *P. platyptera* only occurs as forma *euryptera*; in June—July it has a rather large maximum.

Nøddebo Pond. *P. platyptera* occurs only in relatively few samples, sporadically through all the years of observation.

Funke Pond. *P. platyptera* is perennial; maxima seem to occur at all seasons of the year; during the summer forma *euryptera* occurs, but always together with forma *typica*; this has its maxima with sexual periods in April—May and October—November; *euryptera* disappears in September; mictic females were not observed. —

Schäffergaards Pond. *P. platyptera* is perennial, but is rare in the summer. At that time only forma *euryptera* is found, disappearing again during the autumn. The typical form is very common from October to May and has a large maximum in November. Curiously enough mictic females were not observed.

1. In almost every pond where explorations have been carried out, *P. platyptera* has been found, mictic females seem to occur all the year round; only in January—February they have not been observed. If there is any regularity, it is only in the occurrence of the first sexual period, which almost invariably occurs during March—April; later on there is no regularity whatever in this respect; sexual periods occur both in June, August, October and November. In some ponds mictic females have been observed in the same year in March, August and November. Beyond doubt the species must therefore be polycyclic in ponds. The forma *euryptera* occurs quite suddenly in the plankton, and does not appear to develop from the forma *typica* by means of transitional stages; it disappears in October—November. DIEFFENBACH states that it is a pronounced stenothermal summer form, a distinct species, especially because the resting-eggs differ in the two species. HARTMANN (1918 p. 213) comes to the same result.

2. *P. platyptera* is also a regular inhabitant of the pelagic region of our largest lakes; here, too, it seems to be perennial; in most of the lakes there occurs a pronounced maximum in spring (temperature, 12—15° C.) in some of them also in the autumn; mictic females have been found in the same year and in the same lake in spring as well as in autumn samples. A very pronounced minimum during the summer, characteristic of all our lakes, seems to show that the species is dicyclic in our lakes. As far as my explorations go, it seems that forma *euryptera* mainly belongs to smaller lakes or larger ponds.

3. *P. platyptera* is one of the very few rotifers which seems adapted to life in very small, often drying, ponds, as well as to life in the pelagic region of even the largest lakes; it is rather peculiar that it seems only to a very slight

degree to vary locally as well as temporally; further investigations may show in what manner forma *euryptera* is connected with forma *typica*, or in other words, whether amictic females may produce forma *euryptera* at high temperatures, a supposition which I for my part find highly problematic.

4. If we remember how intimately the occurrence of mictic females among the rotifers seems to be associated with distinct seasons of the year, it is highly remarkable that we here have to do with a species where mictic females seem to appear at almost all seasons and at all temperatures.

5. It may further be pointed out that the male eggs are commonly carried by very small individuals with smooth spines and a sharply pointed posterior part of the body; one of these mictic females is figured by Hudson-Gosse. It really seems as if we here have to do with a conspicuous difference between amictic and mictic females. As, however, all newly born females have the appearance of the male-egg-carrying females, and as the resting-eggs are carried by larger ones with an almost rectangular outline, it would seem a more probable supposition that the mictic females are born and begin egg-production at an earlier stage than the amictic ones, and slowly grow up to the normal rectangular form, in which, if fertilized, they carry the resting-eggs. —

Plate XI, fig. 7—9 shows the three sorts of eggs. Fig. 7 shows how large the parthenogenetic female egg is in comparison with the female itself. The size of the eggs differs very much and often male eggs are found which are much smaller than those figured. Characteristic of the eggs is the great amount of oil globules. Both sorts of eggs, the female as well as the male eggs, are carried by the females but as the females are pelagic, the oil globules may have significance as diminishing the weight of the eggs. The female eggs have often a fine blue colour.

The resting-eggs are very large; the egg-shell is furnished with numerous spines terminating in two curved spines so that the whole spine is really anchorshaped.

#### ***Anarthra aptera* Hood.**

In Fredensborg Pond. *A. aptera* occurs regularly as a summer form; the maximum is always small. It has fairly often been found in May—June in several ponds. It is an extremely slow swimmer, carrying a single large summer egg. Mictic females have never been observed. — Curiously enough LUCKS (1912 p. 43) maintains that it is a stenothermal winter form; my results differ rather from those of earlier authors.

According to the very interesting observations of OLOFSSON (1918 p. 573) it seems that *A. aptera* is only a form of *Polyarthra platyptera*. He has observed that eggs carried by *A. aptera*, contained embryos with well-developed transversely striped muscles and “sogar einige der Lateralanhänge, zu deren Bewegung diese Muskel bestimmt sind.” He regards this as a proof of the supposition that these two forms belong together. The observations have never been corroborated, and the eggs have

not been hatched. — OLOFSSEN combines his observations with very extensive deductions, but I should think it best to postpone such till more thorough investigations have been carried out.

### Rattulidæ.

Of the two genera *Diurella* and *Rattulus* I have only very few observations, especially of the first-named genus. The species are almost all pond-forms; in the winter-months I have never met with maxima and even in the summer-months when the species have almost exclusively been observed, the maxima always seem to be relatively small. On the algæ coatings where the Notommatidæ were often found with great maxima, various *Diurella* species were occasionally observed (especially *D. porcellus* (Gosse), *D. tigris* (O. F. M.), *D. cavia* (Gosse) and *D. brachyura* (Gosse)). The eggs were laid on the underside of the coatings. Most probably they had their maxima at this time, but I never succeeded in finding male eggs or males. —

A few species belong to the central parts of smaller lakes free from vegetation, and a couple belong to the pelagic region of larger lakes.

The two species *Diurella tenuior* (Gosse) and *D. stylata* Eyfert are pronounced plancton organisms, *D. stylata* mainly in larger lakes.

None of these species carry their eggs, they are deposited on other plancton organisms, those of *D. tenuior* often on *Melosira* threads, where already APSTEIN found *Diurella* eggs. *D. stylata*, which mainly belongs to smaller lakes, very often deposits its summer eggs on *Brachionus* species, especially *B. angularis*.

The same is said to be the case with *D. tenuior* (Gosse) and perhaps *D. tigris* (O. F. M)). It is this species which APSTEIN has observed in the Ploener lakes and the eggs of which are found on *Melosira*.

### *Diurella stylata* Eyfert. = *Rattulus bicornis* Western.

Plate III, fig. 3—6.

*D. stylata* is a fairly common plancton organism in the pelagic region of our larger lakes, and very common in the central parts of our ponds free from vegetation. It is a typical summer form, appearing in May and disappearing again in October. It never carries its eggs which are deposited on other plancton organisms; in one of the ponds *Brachionus angularis* was covered with eggs which, when hatched, gave *D. stylata*. In one of the ponds in the Strødam Reservation a large maximum was found in the last days of August. The animal totally disappeared before the middle of September. During the maximum I did not succeed in finding the organism on which the eggs were deposited; *B. angularis* was very rare in the pond at that time. The animal may have had a sexual period since in a few of the specimens I found an egg with a squamate surface figured in Pl. III, fig. 6. The animal itself has been figured in Pl. III, fig. 3 especially to show the enormous retrocerebral organ which seemed to have a glandular organ with two nuclei at the apex.

### **Diurella tenuior.**

Plate III, fig. 1—2.

*Diurella tenuior* is a typical summer form in the pelagic region in many of our lakes. It was mentioned already by APSTEIN (1896 p. 160) from the Ploener lakes and has often been found later on. It has often been determined as *D. tigris*; perhaps both species may be found in the pelagic region of larger lakes. None of these species carry their eggs; they are deposited on other plancton organisms, especially *Melosira*-threads, where already APSTEIN found them, and on which I have often observed them. A sample from July from Tjustrup lake contained numerous specimens of a *Diurella* with two anterior thorns and three posterior ones of different length. It seems identical with *D. Porcellus* Gosse, and with the drawings published by JENNINGS (1903 Pl. II, figs. 19—23) and by TESSIN (1886 Pl. I, fig. 13). The specimens often contained fully developed eggs, and eggs of quite the same appearance were also found on the Dinobryum colonies. On Pl. III, figs. 1—2 illustrate the species and the egg. The reservoir for the food-glands always contains a yellowish brown mass of a peculiar form, which flows out along the spines and often forms a long curled thread from the apex of the longest spine. The egg has many oil globules. We have here, as so often, an example of a typical bottom organism which for a short time during the summer gets out into the pelagic region of lakes and ponds. — But in this case we cannot show that the period in the pelagic region is identical with a sexual period. The males of the genus *Diurella* are so far unknown.

### **Rattulus.**

Of the many *Rattulus* species I have found the following round Hillerød: *R. cylindricus* Imh. (= *Mastigocerca hamata* Zach. = *M. setifera* Lauterb.). *R. capuzinus* (Wierz. and Zacharias). *R. longiseta* (Schranck) (= *Mastigocerca bicornis* Hudson-Gosse). *R. carinatus* (Lamarck). *R. rattus* (O. F. M.). *R. stylatus* (Gosse) *R. pusillus* (Lauterborn).

Apart from the two first-named species, all the others belong mainly to the vegetation in small ponds or small lakes. Most of the species may be found the whole year round, but in the winter-months they only occur in small number. In the summer-months I have seen large maxima of *R. stylatus* and *R. pusillus*, *R. longiseta*, *R. carinatus* and succeeded in finding the males of the two first-named species. The maximum of *R. pusillus* most probably occurred in connection with the algae coverings on the pond. In May—July many of the ponds had large maxima of *R. carinatus* and *R. longiseta*. The species were isolated in many hundreds of specimens, lived some weeks in the cultures, but died out without showing any sign of sexual periods.

**R. cylindricus** Imhof.

Plate III, fig. 7—10.

According to my experience *R. cylindricus* (Imhof) is a true plancton organism occurring in the pelagic region of ponds and smaller lakes, especially those with peaty water. As LAUTERBORN (1908 p. 581) has maintained, it swims round in a gelatinous coating through which the long seta protrudes. It has its maximum at the highest temperature, does not appear until June, and disappears already in September; (LUCKS says already in July (1912 p. 70)); it is a typical monocyclic, stenothermal summer form. It is rather rare, but where it occurs it may form a prominent part of the plancton during the maximum; during this time the plancton gets a very peculiar appearance. In this period the animal carries its eggs. My main locality is the Klare Lake near Hellebæk and the Horshoe Pond.

In the last-named locality it was especially very common in 1929; it appeared in July together with a large Cyanophyceae maximum; mictic females appeared 20/VIII and disappeared again in the first part of September; the amictic as well as the mictic females carried the eggs; females with dark eggs were found but I do not know where the resting-eggs are deposited; perhaps they drop to the bottom.

**R. capuzinus** Wierz. & Zach.

Plate III, fig. 11—15. Plate IX, fig. 15.

*R. capuzinus* (Wierz. & Zach.) is a typical plancton organism of our lakes but also occurs in smaller lakes or ponds. It is a monocyclic stenothermal summer form; it appears in May and may be found even in October. Only very rarely have I seen larger maxima (Hestesko Pond 20/VIII 29), and even then it does not seem to carry its eggs. LAUTERBORN (1898 p. 180) maintains that the eggs are deposited on other plancton organisms, especially *Asplanchna*. LUCKS (1912 p. 72) has found the resting egg in the empty lorica and supposes that it is not deposited. Curiously enough I have not been fortunate enough to find the parthenogenetic eggs; in the samples from 2/IX 29 Hestesko Pond very many *R. capuzinus* were found. Most of them were mictic females with a broad dark band in the last third part of the body. The band was the dark vitellarium. In one of the females an egg was found; suddenly the egg was pushed out of the oviducts and lay for a few minutes agglutinated to the posterior part of the body; then it dropped off; it had no gelatinous cover and is most probably dropped off in the water.

Fig. 13 shows the egg in the animal a few minutes before it was laid.

**Rattulus pusillus** (Lauterborn).

Plate VI, fig. 11—12.

*Rattulus pusillus* is a small species common in many of our small ponds and mainly among vegetation. In a little pond near Sorø *Brachionus angularis* was en-

tirely covered with small rotifer eggs (25/VIII 29). I supposed that, when hatched, they would as usual give *Diurella stylata*. Simultaneously *R. pusillus*, was found in the plancton.

Under the microscope I saw the species rotate round the *Brachionus*; some of them were isolated, and a few hours later many *R. pusillus* were hatched. It was then seen that also this species has a stage during its maximum in which it lives pelagically, laying its eggs on other plancton organisms. The *Brachionus* specimens were entirely covered with eggs. It was further observed that the specimens carried three sorts of eggs, their own large female eggs and the eggs of *Rattulus*, female as well as male eggs. Under the microscope the males, when hatched from the eggs, were observed to encircle the *Brachionus* and their own females, often fastened with a thread to the *Brachionus* carapace. Often the unfortunate *B. angularis* would carry two of their own large eggs, 10—12 female eggs, and 6—8 male eggs of *Rattulus*. Of the whole carapace of the *Brachionus* hardly anything was to be seen. The phenomenon did not last for more than a fortnight; before the end of August the *Rattulus* maximum disappeared, the foreign eggs dropped off the carapace, and the *Brachionus* were deprived of their burden. —

When we referred to the literature, we stated that already LUCKS (1912 p. 64) had found *R. pusillus*-eggs on *Brachionus angularis*. LUCKS, however, maintains that *B. angularis* "bei einem Schleimschicht umgeben ist" and supposes that it is quite accidental that the eggs of the Rattulidæ are hanging in the gelatinous cover. As I have seen *Diurella* species, especially *D. stylata* as well as now also *R. pusillus*, creeping on the *Brachionidæ*, I do not think this supposition is correct. In four different ponds I have year after year seen the *B. angularis* carry their heavy burden of their own and others' eggs; they are all covered with these cuckoo eggs; the phenomenon is too common for it to be accidental. And it may perhaps be remembered that already EHRENBURG (1838 p. 434) and WEISSE (1851 p. 299) observed eggs of *Notommata granulata* on the carapace of *B. angularis* and *pala*.

### Dinocharidæ.

Of the family *Dinocharidæ* the genus *Polychaetus* with *P. collinsi* (Gosse) has always been observed only in small number in small ponds. Of the genus *Dinocharis*, *D. tetractis* Ehrbg. and *D. pocillum* (Müll.) have been observed almost in all ponds where explorations have been carried out; distinct maxima or males have, however, never been observed. —

Of the genus *Scaridium*, *S. longicaudatum* Ehrbg. is not rare in smaller ponds rich in vegetation, and with peaty water. It is a pronounced summer form, mainly occurring at the highest temperature of the water. A single time in a little bog I found (20/VII 25) in the central part of a hole, only a few sq. m. large, a peculiar "plancton" of numerous *S. longicaudatum*. The bog almost only contained this species. The plancton, with these numerous always jumping specimens, had a

peculiar appearance. Though I eagerly searched for males, male eggs or resting-eggs they were not observed, and I was obliged to leave the locality before a sexual period set in. —

#### Salpinadæ.

Of the Salpinadæ large maxima formed by members of the genus *Salpina* have several times been observed. This is especially the case with *S. mucronata* (O. F. Müller) *S. brevispina* (Ehrbg.) and *S. spinigera* (Ehrbg.). Maxima have always been seen in spring; mainly in inundated localities or at the borders of ponds with an unusually high water-level. Using the net over the inundated grasses, enormous numbers of *Salpina* specimens may often be gathered.

When the material has sedimented, the water may be coloured milky with *Salpina* specimens, *S. mucronata* especially being present almost in pure culture. In spite of the enormous numbers, and though the locality was under regular observation almost every fourth day, only extremely few males were observed, and all eggs deposited or thrown out over the bottom were amictic. Already before the end of May the development was stopped, and later on the specimens of the different species were only observed in relatively modest numbers.

#### Euchlanidæ.

Of the *Euchlanidæ* I have only observations with regard to the genus *Euchlanis*; of the species belonging to this genus *E. dilatata* Ehrbg., *E. oropha* Gosse (= *parva* Rousselet) *E. triquetra* Ehrbg. und *E. lyra* Hudson have often been found.

Most of the *Euchlanis* species belong to small ponds rich in vegetation; they mainly occur in the summer-months, in most of the samples their number is not great. In May 1924, in a locality which is inundated every spring but is always dry during the summer, I found *E. triquetra* with a great maximum in some of the small waterfilled hollows. Most of them were only about one square meter in diameter and one dcm. deep. Males were common, and mictic females depositing male eggs in the vessels very numerous. Before June the hollows were desiccated and got no water before next spring. Active life can only have been possible for a month, the locality being ice-covered till about 15/IV.

The species *E. dilatata* and *lyra* as well as other species were often seen during the summer-months; males were observed in May—June.

In the pelagic region of our lakes we often find a small *Euchlanis* species which I have referred to *E. oropha* Gosse (= *parva* Rousselet). It belongs mainly to the pelagic region in late summer and autumn. In September 1925, on an excursion on Esrom Lake, on shaking *Myriophyllum* in a plancton net No. 20, it could be seen that the sample contained innumerable quantities of this species. The material was taken from the outer part of the *Myriophyllum* zone some 75 m. from the shore, forming the outermost part of the visible vegetation in the lake; the long green garlands were floating in the surface of the lake. It was these

garlands which were taken up and shaken, and the material brought into the laboratory.

When the material had sedimented, the water was coloured milky with the species. The next day, when plancton samples were taken in the pelagic region only about 25 m. from the borders of the vegetation, the sample teemed with *Euchlanis* which formed a peculiar plancton, most probably never previously observed in a lake about 30 □ kil. large and about 30 m. deep. In the central part of the lake about 1 kil. from the shore, the number of *Euchlanis* was not considerably higher than in other lakes. The garlands were now studied till December. During all that time the *Euchlanis* could be found there, but the large maximum did not last beyond the 15. November. The next year, when the *Myriophyllum* garlands reached the surface in July, the *Euchlanis* were common and again got their huge maxima in September—October.

In the vessels enormous numbers of eggs, male eggs as well as amictic ones, were thrown upon the bottom. Most probably no one has suspected that an *Euchlanis* species has its real home in the outer part of the vegetation zone of our larger lakes, and there lives a short semipelagic life during the sexual period. — LUCKS (1912 p. 100) states that the *Euchlanis* species, especially *E. dilatata*, is common in the pelagic region, and that the eggs are deposited on limnetic algæ; they may also occur here, swimming (1912 p. 102).

Of the genera *Cathypna* and *Monostyla* large maxima have sometimes been observed, especially in very small hollows covered with vegetation; this holds good especially with regard to *C. luna* (O. F. Müller), *Monostyla cornuta* (O. F. Müller) and *M. lunaris* Ehrbg. The maxima were always observed in the summer-months. Males and sexual periods have never been seen.

#### Colurellidæ.

Specimens belonging to the two genera *Colurella* and *Metopidia* have often been met with.

They almost all belong to small ponds rich in vegetation. The species *Colurella bicuspidata* Ehrbg., *Metopidia triptera* Ehrbg. and *M. lepadella* Ehrbg. have been observed in enormous numbers, especially in early spring. WESCHÉ has found the male of *Metopidia lepadella* already in February.

They all belong to very small ponds and ditches covered with a scum of algæ. It seems as if some of the species have very restricted maxima in late spring and early summer.

The very peculiar species of the genus *Stephanops*, *S. longispinatus* Tatem, *S. lamellaris* (Müller) and *S. cirratus* (Müller) have only been observed in small number in the samples; hitherto they have only been seen during the summer-months.



### Anapodidæ

comprises the three genera *Ascomorpha*, *Anapus* and *Sacculus*. To *Ascomorpha* is referred *Ascomorpha agilis* Zach., to *Sacculus* *S. viridis* Gosse, to *Anapus* two species *A. testudo* Lauterb. and *A. ovalis* Bergend. The affinity between these forms is very doubtful.

#### *Ascomorpha agilis* Zach.

Plate IV, fig. 1—9.

*Ascomorpha agilis*, which seems to be rather rare in other countries, is a regular inhabitant of smaller lakes and larger ponds in Denmark. It has been found in the pelagic region of our largest lakes in Furesø, Tjustrup Sø and in Haldsø; here, however, always as a summer form, always sporadically, and always together with large *Ceratium maxima*. In the series of ponds in which regular explorations have been carried out it has only been found in a few samples in most of them. In others it has often had an enormous maximum; bluish-black as it is, it may colour the samples almost black; this has been the case with bog-holes in the so-called Clausens moor, in Funke Pond, and in ponds near Sorø.

It seems especially to belong to peaty water; here its maximum coincides with that of the spring maximum of *Peridinium tabulatum*, *Uroglena* and *Dinobryum*. Where it has been more thoroughly observed, the maximum begins in the middle of April and already in the middle of May the species has disappeared. During the maxima the samples have almost been black with *Ascomorpha*, and already about 15/V not a single individual could be observed in samples from the same locality. — Now and then e. g. in Funke Pond (1909) a rather large maximum may also be seen in July, August and in some ponds (Strødam) enormous maxima occurred in November; the main maxima seem however almost always to occur in early spring. The animals get their food in the following rather peculiar way. The flagellata especially *Peridinium* and *Ceratium* are seized by means of the unci; the mouth parts pierce a hole in the carapace whereupon the flagellate is sucked out; the yellowish green contents are swallowed down into the very large stomach, which is coloured dark green.

Though I have often observed the large maxima and during these have taken samples every fourth day, I have only very rarely seen the males<sup>1)</sup>. The females never carry their eggs, the eggs are deposited on other plancton organisms, especially Flagellata, occasionally *Dinobryum*, but mainly *Uroglena volvox*; the latter may often, during the huge maxima of *Ascomorpha*, carry several eggs. Any pronounced difference in size between these eggs I have not been able to see; before the maxi-

<sup>1)</sup> In my Plancton Investigations, 1904 p. 139, I have maintained that I had found the males in countless numbers in April. This may be incorrect, and may be referred to the just hatched young ones, which are very small and quite hyaline.

imum of *Ascomorpha*, was at an end, that of *Uroglena* had finished, and I was never fortunate enough to see where the resting egg was deposited.

During the last part of the maximum females were found with a large globular thickshelled egg in the oviduct most probably these eggs are dropped to the bottom. They were not to be found upon the *Uroglena* and not in the empty shells. When the maximum was at an end, empty carapaces containing bluish black bodies, the residua of the stomach, were extremely common. As far as I can see, the animals have no anus.

*Ascomorpha agilis* has always been rather badly studied. Fig. 3 gives a sketch of the lorica, the most pronounced folds in the skin, and the dorsal organ. The forepart with the folds can be folded together, leaving only a sharp thorn dorsally.

When the wheel organ is fully unfolded, it is of a rather complicated structure. Peculiar is especially the strongly developed bill-shaped antenna whose form, however, is subject to great variation; it seems to be able in some degree to be drawn in; the mastax is very large, globular and furnished behind with a very large body of glandular structure containing a single large whitish spot whose structure is rather problematic. The mouth-parts (fig. 5) are of the virgate type and may be protruded into the mouth-opening the sides of which may be prolonged, tubelike, and dentate at the edge. The oesophagus begins dorsally; it is short and runs to the enormous stomach which fills most of the body cavity. Most probably the digestion is intracellular, the cells of the stomach are overfilled with rests of chromatophores. The stomach itself contains large bluish-black or black residua from the nutrition; as far as I can see, there is no anus, and no cilia upon the stomach cells. The residua are not thrown out through the mouth, but remain in the empty carapace after the death of the animal. Two small gastral glands are present. When the animal is well-fed, the structure of the stomach cannot be studied, but if kept on inanition for a few days, it may be shown that it is built up of rather large cells (fig. 1). I have only succeeded in seeing a little of the excretory canals and no vibratile tags. The contractile vesicle is large, opening dorsally. The ovary presents itself now as a globular mass, now more bandlike; it has most probably eight nuclei. The brain is large, a retrocerebral organ is not observed, nor any lateral organs, only a dorsal organ. The two sorts of eggs have been shown in fig. 2 and fig. 6. Highly characteristic of the animal is the bluish-black colour.

### **Sacculus viridis** Gosse.

Plate IV, fig. 10—16.

Nowadays most of the authors are inclined in the genus *Ascomorpha* to include two species *Ascomorpha ecaudis* Perty (= *Sacculus viridis* Gosse) and *Ascomorpha agilis* Zacharias with the closely allied *A. saltans* Bartsch and a new species,

*A. minima* v. Hofsten. As far as I can see, the two main species *A. ecaudis* and *A. agilis* differ in all essential points. *A. ecaudis* has a very thin skin, no lorica, no antenna, and carries its eggs. *A. agilis* has a well-marked lorica with a very peculiar folding apparatus in front, a thick fleshy antenna; the eggs are deposited on other plancton organisms. *A. ecaudis* swallows its prey, putting it down into its enormous stomach; *A. agilis* sucks it out, the mouth-parts being protruded from the mouth. Both species have no foot, but, as is well known, this is of no systematic significance. — The systematic position of the two forms cannot at present be determined but it is presumably not correct to include them in the same genus.

*Sacculus viridis* is rather common in small ponds and in ditches filled with vegetation; the amictic females carry their eggs (1—2) and the mictic the numerous (10—12) male eggs. Females with a very large resting egg within the oviduct have several times been observed. Deposited resting-eggs have not been observed. *S. v.* appears in April—May shortly after the ice has disappeared; large maxima have only been observed a single time, (May 1929, Funke Pond); it seems to be commonest in early spring; mictic females have been observed from April to October.

The anatomical structure of *Sacculus viridis* has always been very superficially studied. It has a peculiar thick, almost swampy, lorica; its form is very irregular, varying according to the contents of the stomach and of the ova. The structure of the wheel organ is seen in the figures. The mastax (fig. 16) is almost globular, with two small mastax glands behind. The mouth-parts are almost regular, virgate. The stomach is enormous, filling the whole body cavity; seen ventrally or dorsally it presents itself as two large lobes surrounding the reproductive organs. The wall of the stomach always contains great amounts of chromatophores, oil globules and bluish-black residua of the food; gastral glands have not been observed; most probably the digestion is intracellular; of the excretory system only the rather small contractile vesicle opening dorsally has been seen; an anus has not been observed. The vitellarium is large, containing eight nuclei; its aspect differs very much in the different specimens; the mictic females may carry about 12 very small male eggs or one single dark resting egg which may be deposited, but where is unknown; fig. 10 shows a female which carries one resting egg and has another under preparation.

#### **Anapus testudo** Lauterborn.

Plate VIII, fig. 28—30.

*A. testudo* is a plancton organism, belonging to the pelagic region of our largest lakes. It is a pronounced summer form, appearing in July and disappearing in September. It always occurs together with the large *Ceratium hirundinella* maximum and disappears with it. In all samples it has only been found in rather scarce number; neither eggs nor sexual periods have been observed. It does not carry its eggs which may most probably be deposited on other plancton organisms. Hitherto it has not been possible to find them.

**A. ovalis** Bergendal.

Plate VIII, fig. 31.

*A. ovalis* Bergend., differing from the almost isodiametric *A. testudo* by its more elongate form, is the substitute of *A. testudo* in small ponds covered with vegetation. It seems to belong to the vegetation zone, often occurring together with *C. cornutum* and *Peridinium* species. It is rather rare, and has only been observed in small number. It does not carry its eggs, and neither eggs nor sexual periods have been observed. Both species have the cells of the stomach overfilled with rests of chromatophores.

It is of some interest to see how a small group of rotifers are in reality temporarily as well as locally intimately associated with another, sharply defined, group of organisms: in casu the Flagellata. All the above-named Anapodidæ feed on Flagellata. *S. viridis* swallows them, *Ascomorpha* and *Anapus* pierce holes in the scales and swim away with their prey, pushing it before them; when sucked out, the empty shells fall to the bottom. The bottom of a vessel with many *Anapus* or *Ascomorpha* will soon be covered with empty scales of Dinoflagellata; one of them, *Ascomorpha agilis*, lays its egg on them, and this may perhaps also be the case with the *Anapus* species.

Characteristic is further the enormous often lobate stomach, always coloured by the Chromatophores of the swallowed Flagellata. As I have never seen a defecation, I suppose that the absence of an anus may be regarded as a family character, the posterior opening being only a urogenital opening; most probable the digestion is intracellular.

Figures 29—31 Plate VIII show the two species, the more elongate *A. ovalis*, and the broader *A. testudo*. I have observed three antennæ in *A. testudo*, but only one in *A. ovalis*. The mouth-parts are of the same type in both, and the stomach contains large amounts of black bodies, remnants of the food. Of the excretory organ only the contractile vesicle has been observed. — *A. testudo* which is a bolder swimmer than *ovalis*, has a better developed wheel organ with large auricles.

**Ordo Brachionida.****Hydatinadæ.**

To the family Hydatinadæ are referred *Hydatina*, *Rhinops*, *Notops* with *N. brachionus*; the last-named species has never been found in our country. Many years ago Dr. ROUSSELET at my request sent me some living *N. brachionus*. The two figures (Plate V, fig. 1—2) give some anatomical details which have not hitherto been given. As the animals have been slightly pressed the posterior outlines do not issue at right angles from the lateral ones.

### *Hydatina senta* Ehrbg.

For a long time, more than several years, I have in vain searched for *Hydatina senta*. During my exploration of many hundred small ponds, scattered over the whole country, but mainly in the north of Seeland, I have only once, in May 1898, found *Hydatina* in a little pond which now and then got manure from a cow-stable through a small drain. Unaware of this latter fact in 1898, I did not understand why *Hydatina* was found just in this little pond and for about 20 years after searched for *Hydatina* in all ponds in the vicinity. In the latter part of May *Hydatina* disappeared from the above-named pond; in the following years the pond got no drain from the stable, and I never found *Hydatina* in the pond again.

In 1921, on 21/IV, *Hydatina* was found in a little ditch, which received several affluxes from a large cow-stable; the water was brown, it contained numerous *Euglenas* and it smelled of manure.

This made me, who was just at that time (1922—24) studying the occurrence of Anophelines in our stables, search for *Hydatina* partly in the stables themselves, partly in manure ditches surrounding the dunghills, and in ditches which were partly filled with water from melting snow and rain, partly with affluxes from the stables. Several times I have found *Hydatina* in the stables themselves, in the cemented watering-troughs. This was especially the case in dirty stables; now and then they were found in the very dark and very ill-smelling mixture of urine and rain-water round the dunghills; quite especially they were however found in the above-named ditches with faintly yellowish water, consisting mainly of rainwater, but with a supply of manure differing from day to day. Furthermore *Hydatina* was found in small ponds and pools near the stables where cattle were watered during the summer, localities which were quite dry in summer and whose bottom was covered in summer and autumn with numerous excrements of geese and ducks.

In early spring liquid manure mixed with water is spurted over the fields. In 1921 and 1922 heavy snow and rain filled with water all the small hollows, which during the following fortnight were scattered over the arable land throughout North Seeland. In these small pools, the size of which did not exceed 100 square metres, the water was often yellowish, owing to the bottom being impregnated with manure. The deepest of these pools which still contained a little water in May, were often covered with coatings of *Euglena*. Now it could be shown that many of these temporary pools contained *Hydatina*. Most of these pools totally disappeared before the latter part of April, all before the first part of May; later on the earth concealed the corn seeds for the following harvest as well as the resting eggs of *Hydatina*. With this observation in mind, in April—May 1923 I visited many similar pools in the middle of Seeland. They almost always contained *Hydatina*, but later on, even if heavy rain filled the pools in summer and autumn, no *Hydatina* appeared. During the following years I could of course get *Hydatina* in unlimited numbers; when they had never been found up to 1921 it was only because

I had never searched for them in the right, and indeed scarcely very pleasant, localities.

In my fresh-water explorations the small water pools in the villages have always played a prominent part; in the first place they contained many very interesting Chlorophyceae and Rotifera, further, members of the genus *Daphnia*, *D. magna*, *D. pulex* and *D. hyalina*, all of which have been studied for years at the laboratory here. It was here too, that my assistant, Mr. Berg, found *D. atkinsoni*. In these ponds *Hydatina* are found now and then; commonly they are rather rare here, and if they are found the ponds almost always get a supply from stables; in spring they are often covered with numerous ducks and geese; the water-level depends totally upon the rainfall, but during the last part of July most of them are laid dry; the muddy bottom is then covered with grasses. Now the peculiar thing is that the *Hydatina* always disappeared from the localities during the middle of May. Even if the ponds contained water much longer, no *Hydatina* were found in the latter part of May.

With regard to my area of exploration there is no doubt that the home of *Hydatina senta* is very small drying up pools and ditches, whose water is mixed with liquid manure, often to such a degree that it may be a yellowish brown. Later on I learned that LAUTERBORN had long ago arrived at a quite similar result with regard to his district. The fact is in accordance with the results gained from laboratory work from the last twenty years (SHULL, WHITNEY).

The other fact which interested me very much, was that in spite of explorations in very many manure ponds and also in such as were filled with water almost the whole year round, *Hydatina* was only in a single case found after the middle of May. Because this rotifer has never been found in localities where regular plancton explorations were carried out nor in such where regular explorations carried out every week are still a desideratum, it is easy to understand why the biology of this rotifer in nature is almost quite unknown. This is so much the more regrettable, because of all wheel-animalcules just this rotifer is the best known in almost every direction, owing to the elaborate investigations of its biology under laboratory conditions.

Since all the localities where I had now found *Hydatina* were every year frozen to the bottom till the latter part of March and often till the first of April, and since, furthermore, the animals, even if the ponds were filled with water, disappeared in the middle of May, it was beyond doubt that the number of generations which *Hydatina* could produce in the laboratory during a year of observation, really could not be found in Nature. Most probably it could not produce more than relatively few generations in Nature. Keeping in mind that WHITNEY has kept *Hydatina* living for  $2\frac{1}{2}$  years, and has during that time cultivated it through more than 500 generations, it will be understood that here we had to do with the most striking difference in behaviour under laboratory and natural life conditions. I have, therefore, followed the life of *Hydatina* in different localities during the years 1921—

1924, samples being taken every eighth and often every fourth day; the localities were visited before the ice had disappeared and until the pools were laid totally dry; several of them got no water before the drifting snow melted the next year. The liquid in which the animals were kept in the laboratory was the natural, non-diluted water of the pond. Observations in ponds and in vessels in the laboratory were always combined. Before entering into my own investigations it will be necessary to give a short sketch based on the literature relating to the investigations carried out on *Hydatina* in culture, of our knowledge of its biology under artificial conditions. According to these investigations carried out in the laboratories the life-history of *Hydatina senta* is there as follows.

When the resting egg is hatched an amictic female invariably appears; this female, if the conditions are good, produces about 50 eggs, which all give rise to other females; already in this second generation, these females may be divided into amictic and mictic females. To find any difference between the two kinds of females has hitherto been impossible.

In the size of the eggs laid by the two sorts of females there is some difference, but it is not great, and we often find intermediate stages, so that the two kinds of eggs are not distinguishable from each other by their size. Females are either amictic or mictic, never both; mictic ones seem especially to appear in the early part of a family of daughters. The number of eggs the two females lay at lower temperatures is almost the same, but at higher temperatures the mictic female produces eggs faster than an amictic one, and also produces more eggs throughout her lifetime. The result is that enormous amounts of males are suddenly produced in a colony, and the phenomenon of male epidemics appears. It has been shown that these epidemics show a regular periodicity in cultures so that the males appear in well-defined "waves"; these "waves" are a culture product, in Nature there is no time to produce more than one "wave". The males may pair with the amictic as well as with the mictic females, but pairing has no influence on the first-named. If paired with a mictic female, the latter will begin to lay resting-eggs in a number of about twelve. It will therefore be understood that the resting-eggs are the fertilized male eggs, and that the mictic females are the sexual females; the sexual eggs are able to develop without fertilization, but then invariably give males.

The resting-eggs may develop in the course of several weeks or may rest for many months. We will now pass on to my own observations in Nature. In the following some of my diary notes are given.

On 5/IV 1921 many ponds and small ditches were still covered with ice. This was also the case with a little ditch two kilometres from Hillerød. When the ice had disappeared, the bottom was quite dry; rain and snow filled the ditch during the days 5/IV—15/IV; from a large cow-stable liquid manure flowed into the ditch, which soon got a yellowish colour; it teemed with Flagellata of different kinds, mainly *Euglena*. In samples taken during my absence at my Sorø laboratory, a few *Hydatina* were taken on 15/IV. Temperature 3° C. On 21/IV the number had

augmented enormously. In the whole ditch there were only a few cubic metres of water; it was water-filled over a distance of about 5 metres; it was only 1—2 decimetres broad and the depth was never more than one decimetre, often less. The surface was covered with green algæ; yellow, withering, half-decayed straws from the last years filled a good deal of the water. The *Hydatina* were present in countless numbers. They were sitting on the straws, covering them with a thick coating; furthermore it could be shown that the water was covered with a rather thin layer of green algæ, on which the animals were creeping about. With the wheel organ pressed against the algal coating by which the animals are nourished, they moved over the underside of the surface; very often they removed the forepart from the film, hanging downwards only supported by a thread spun of material from their caudal glands. During the time 15/IV—21/IV countless numbers of resting-eggs deposited last year must have developed; the material contained almost only amictic females, but a few males were observed. In the vessels the surface was covered with a thick layer of algæ; already on 22/IV it contained numerous small whitish stains a sq. cm. in size, consisting of male and female eggs, the former much smaller than the latter. Everywhere from the surface the females were hanging down, whirling organisms into their mouths by means of the wheel-organ. Many females were creeping about on the layer or were depositing eggs. In vessels in which the algæ coating on the surface is regularly removed, the eggs are laid on the sides of the vessels and on straws; in these cases the colony soon died out. On the egg spots the females, commonly five to ten, were almost always in activity; the spots often contained about fifty to seventy eggs. When the vessel was placed in the window or otherwise with strong one-sided illumination, this had no influence upon the animals; as is the case with so many often benthonic rotifers, *Hydatina* is by no means positively heliotropic. The males creep round the egg spots, often over the females; pairing is often observed, always through the skin, never through the cloaca.

Already on 23/IV the colour of the white spots is somewhat altered; observed under the microscope they now appear "pepper and salt" coloured; this is due to the great number of resting-eggs. On 25/IV almost all female and male eggs are hatched and resting-eggs in countless numbers are spread over the underside of the algæ carpet. This carpet augments in thickness from day to day, consisting of a peculiar thick jelly, which I first supposed was derived from the algæ. By 27/IV only resting-eggs are found; the females diminish in number; the males are still rather common, often sitting with the foot in the empty egg-shell. Before 1/V almost all animals had perished but below the surface were scattered many thousands of resting-eggs. During the whole time from 21/IV to 27/IV the water was not changed; its colour was yellowish without any smell.

The localities are visited again on 27/IV. During the days 24/IV—27/IV it has rained very much; the water-level in the ditch is much higher, and there is no algal cover on the surface; the water is clearer and beyond all doubt strongly



diluted. The number of *Hydatina* is still enormous; in the new samples the surface is again during the night covered by a green jelly, in which there are many algæ. That night 32 small egg-spots were formed, each containing 200—300 eggs. Most of these eggs are female eggs, some resting-eggs, but not so many male eggs. If an egg spot was taken from the film, it contained as many as 180 egg-laying females and 20—30 males. Isolated egg-spots without animals are hatched the next day; about 30—35% are males. The eggs therefore require a temperature of 12° C. in the vessels and take, for hatching, at all events not more than 24 hours. In the following time, from 28/IV—20/V, the locality is visited three times; *Hydatina* is always found, but in decreasing number. By 20/V there is very little water in the ditch, by the last week of May it is totally desiccated. During June—December I have very often passed the locality in my motor-car; rain has several times filled the ditch, but no *Hydatina* were discovered. On the grass and at the bottom are found numerous resting-eggs. During the time 15/V—1/VI all my cultures almost die out entirely; the film on the surface of the water is covered with thousands of resting-eggs, but curiously enough during the whole summer I always find very few females in the vessels; instead of thousands in April, now only about 20—30.

On 5/XI the ditch is filled with snow, and a frost period begins; the ponds are covered with thin ice. On 3/XII most of the ponds are open again; during December the air-temperature lies between 1½—2½° C. On 24/XII the ditch is found filled with rather clear water, derived from melting snow; the temperature of the water is 1° C. Now several *Hydatina* are found and among them curiously enough a few males, hatched at this very low temperature. On 15/XII the same is the case, but on 31/XII all ponds and ditches are covered with ice. During the time 31/XII 1921—15/III 1922, all ponds and ditches are covered with thick ice and snow. The *Hydatina*-ditch is open on 15/III and at a water-temperature of + 4° C. gives very many *Hydatina*, all females. Then frost sets in again and the ditch is frozen to the bottom from 15/III to about 1/IV. During this period it seems as if all *Hydatina* have been killed. Often as I visited the ditch in 1923 I never saw a single *Hydatina*.

In a little very dirty pond, Fredensborg Castle Pond, *Hydatina* was found in 1921. The pond was at that period rather clear and contained many green algæ. In the spring it is about ½ metre deep, and never desiccates totally. It contains the little fish *Leucaspius delineatus*. The pond has not the slightest vegetation and during summer is covered with a thick layer of blue-green algæ. *Hydatina* was common in the plancton in 1921 together with *Rhinops* and many other rotifers. It lived here as a real plancton organism, and had its well marked sexual period in the latter part of May, whereupon it totally disappeared before June, together with *Rhinops*.

In 1922 the pond got an afflux from a very dirty sewer, the water in the pond was now greyish and almost all rotifers died out. *Hydatina* was not found in 1922 nor in 1923; but curiously enough it appears again on 23/VII 1923 and

is then found in almost all samples till 20/IX. In some of the samples it is rather common, but males are never seen, and when taken into the laboratory the females only produce large eggs, never male eggs. It seemed as if only amictic females appeared; I presume that mictic females have appeared in the autumn, and that a short and feeble sexual period has escaped my attention.

In the little Endrup Pond, near Fredensborg between Esrom Lake and the Sound, *Hydatina* was found during the spring of 1922, later on in the year it disappeared. The pond is very shallow and in warm summers is often laid dry; it gets affluxes from the farm-yards in the neighbourhood. It contains no higher plants, but the water is always coloured by huge maxima of *Chlorophyceæ* and *Flagellata*; the depth never exceeds  $\frac{3}{4}$  metre. In the summer it is almost always dry and the bottom covered with grass, on which numerous ducks and geese drop their excrements. During severe winters it will most probably always freeze to the bottom; in June, immediately before desiccation, the temperature may rise to  $24^{\circ}$ — $25^{\circ}$  C. Apart from *Chlorophyceæ* and *Flagellata* the pond contains a very rich plancton of *Brachionus* and *Daphnia magna*.

In 1923 the pond was visited on 9/IV. During a long period the temperature of the air had been about 0, and Endrup Pond was still ice-covered on 11/IV in the morning. At 12 o'clock it had almost thawed owing to the bright sunshine. On 11/IV the temperature rose to  $6^{\circ}$ — $7^{\circ}$ . Not a single *Hydatina* was found in the plancton, but on the stones and in their coatings of algæ numerous *Hydatina* occurred. On 22/IV the pond showed very remarkable phenomena. It was calm, bright sunshine and the temperature of the water over the stones was  $18^{\circ}$  C. Air-temperature  $12^{\circ}$ . The pond was covered with a coating of blue-green algæ; the surface showed peculiar drawings of concentric lines, blown eastwards; between most of them were very small intervals near the shore and larger ones nearer the middle of the pond. The concentric lines were darker than the intervals. A more thorough exploration showed that the lines were almost entirely made up of innumerable masses of *Hydatina*-eggs. A plancton-net gave *Hydatina* in almost incredible numbers. The same was the case with the coating of algæ on the stones, which, when shaken down in the net, gave almost pure cultures of *Hydatina*. In the plancton males as well as females were found.

On 25/IV the pond was visited again; the concentric rings had now disappeared, but everywhere the pond teemed with *Hydatina* in the plancton as well as on the stones. On 3/V the number was most probably the same, but on 8/V it had diminished very remarkably; no males were observed; no specimens were found in the plancton, and the females were now only found creeping on the stones. On 21/V *Hydatina* was very rare, and later on it was not observed during the rest of the year. The pond had water almost the whole summer but was totally desiccated in September—October. —

During the winter of 1923—24 all ponds were frozen from the last part of November to the first part of April. On 10/IV 24 Endrup Pond was open, but

many other ponds were still ice-covered. No *Hydatina* in Endrup Pond; the same is the case on 19/IV, when the temperature of the water is only 3° C., (air-temperature 2°—5° C.); furthermore on 5/V, when the temperature of the water and the air is only 5° C. On 16/V *Hydatina* is found again; not so numerous indeed as in 1923, but very common on the stones and living simultaneously as a plancton organism in the central parts of the pond. On 28/V all *Hydatina* have disappeared. The pond is filled with water, at all events through the whole of June—July and the greater part of August. The observations are repeated in 1924 and give quite the same result. The observations carried out in the vessels in 1923 may now be augmented by the following. When the vessels were filled with material from Endrup Pond during the period 22/IV to 1/V and countless *Hydatina* filled the water, the surface of the water would the next day be covered with a remarkably thick jelly. I supposed that this was in the first place due to Algæ, but Professor MARTINI, who was at that time working at the laboratory, thought that it was derived from the Rotifera. Observations in the following days showed that this was really the case. During the following days, thick threads went down from the surface to the bottom of the vessels; these threads were interwoven, and during the following week a regular network was formed. Along these threads the *Hydatina* wandered up and down, or they would sit on the threads, whirling food in their wheel-organ. The eggs were always deposited on the surface. It must be remembered that the *Hydatina* of both sexes are provided with unusually large and broad caudal glands. Wherever the *Hydatina* moved, they drew a long gelatinous thread after them; the thread was also visible when they swam, though not as a thread but as a long series of particles of detritus moving together with the animals. All these threads swell in the water, adhere to each other, and hang down from the thick coating on the surface of the water, which serves as a substratum for the animals and on which the eggs are deposited. It is the same material which was observed on 22/IV in concentric circles on the surface of Endrup Pond.

It seems as if the animals, when living in larger ponds during the sexual period, may partly live a short semipelagic life. Most probably the countless numbers of animals, living on the stones near the border of the ponds, spin large quantities of threads there, by which they are carried out over the surface of the pond, and from which they subsequently free themselves. In the night when the countless numbers of threads become glued to each other, they form, with the algæ, and their gelatinous coatings the surface-film of jelly on which the eggs are laid, and which is broken later on by the first morning breeze, and swept into the small bays of the pond. —

Twice during the August of 1925 when the air-temperature was 20°—22° C., and the water-temperature 24°—26° C., I traversed a good deal of Seeland in my motor-car and took about 20 samples a day in village ponds and in ditches; all the samples were brought living to the laboratory. My object was to make sure that such organisms as *Hydatina* and *Rhinops* really had totally disappeared during

the summer. Out of these about 40 samples only one single one contained *Hydatina*, and that only in very few specimens; these were always females and always animals which only produced females in the vessels, i. e. amictic females. In 1929 I found a new pond in which I again saw a few *Hydatina* in June. On an excursion I found *Hydatina* in another little pond at Søllerød about 14 kilometres south of Hillerød. It was found in great number on 8/VII 1923; in this case, too, there were only amictic females; the pond was again visited on 18/VII and three times at regular intervals in August; but sad to say the samples contained not a single *Hydatina*, I was accordingly prevented from observing whether these females could be forced to develop mictic individuals.

During the winter of 1929—1930 the ponds were not frozen before the last days of January. Owing to the peculiar forms of *Brachionus pala* a new pond, Bistrup Pond, was regularly visited from July 1929; by 11/IX a single amictic female of *Hydatina* was found; it was then observed in a single specimen 3/XII and 8/I. By 31/I, when the pond was covered with ice, very few females were observed. In this and similar cases it seems that a few resting-eggs may be hatched before winter sets in but that the females hatched from these eggs propagate extremely slowly. A few females appeared in April 1930, but later on no females were found.

If now, from the explorations carried out in Nature, we try to sketch a picture of the life of *Hydatina senta* under natural conditions and in our latitudes, we shall arrive at the following results.

1. In the first place it is beyond doubt that the real home of *Hydatina* is in very dirty waters rich in organic matter, and especially such waters as have affluxes from stables or sewers. In water which is a deep yellow and whose colour is derived from liquid manure it thrives exceedingly well; its main food here is green Flagellata, which colour the stomach a vivid green. These results are in full accord with those of LAUTERBORN (1898).

2. Furthermore it may be regarded as an established fact that *Hydatina* belongs mainly to drying ponds, often to localities which do not get water every year, and in dry summers only for a few months. The water is commonly derived from melting snow or from the rainfall in early spring; the organic matter which seems a life condition to this species and more especially the manure of the previous year comes from the bottom, the bottom being impregnated with liquid manure or covered with excrements of ducks, geese, sheep etc.; in spring the localities often get a new supply of manure.

3. Now and then *Hydatina* may be found in permanent ponds, but only very rarely, and then only where the water in some way, e. g. through sewers, gets a rich supply of organic material.

4. *Hydatina* is mainly a bottom-organism which, half creeping half swimming, moves over the bottom of the pond, and especially over the coating of algæ covering the stones of sunny shores at the water's edge. From the littoral it moves out over the surface of the pond, creeping on the underside of the surface-film, using

it as a substratum. By means of the gelatinous secretion deriving from its unusually large pedal glands, it augments the thickness of the film itself. This film contains enormous masses of unicellular green algæ, especially Flagellata, which, at all events in my localities, form the main part of its food.

5. During the sexual period *Hydatina* may leave the substratum and for a short time live a semipelagic life together with the other rotifers of the locality, (*Anuræa*-, *Brachionus*-species and very often *Rhinops vitrea*). The semipelagic condition is a necessary result of heavy showers and strong winds which break or dilute the film of the surface.

6. Most of the eggs are deposited on the film, presenting themselves as whitish spots; each spot is the result of the activity of many females surrounded by the males which creep about over the egg-spots and between the females. When the active life of the stock is at an end, all deposited eggs are resting-eggs, which are sooner or later swept to the borders of the pond or sink to the bottom.

7. It is a highly remarkable fact that, even if the pond contains water either the whole year round or at all events until August, the active life of the whole stock is often restricted to only six or eight weeks, almost always in early spring, in our latitudes mainly in April—May. In all the other months the organisms live a latent life as resting-eggs on the floor of the pond. In this respect they behave like several other organisms belonging to drying ponds, but mainly to such, whose water is clear and the bottom of which is covered with a rich green vegetation.

8. During this exceedingly short time the number of generations cannot of course be very large. According to the excellent laboratory-studies of *Nussbaum* a. o. the average lifetime of a *Hydatina* may be stated to be about 9 days. Using this and the other well known facts relating to the biology of *Hydatina*: number of eggs (about 50), the number of days before the newly born female is able to produce eggs (1—2), number of hours before the female lays its next egg, we are able to calculate that in numerous localities and in many years the number of proterogen (PAPANICOLAU 1910 b p. 739) generations will be between ca. six and ca. thirty.

9. As the eggs only take a day to develop and the hatched females are ready to lay eggs almost on the day on which they are born, the size of the generations is augmented enormously from day to day, a series of generations deriving from these proterogene generations are therefore "working" simultaneously.

10. It has been shown that in the course of only a week the ponds may teem with *Hydatina*. This may in the first place be due to a rather sudden and simultaneous hatching of resting-eggs. Even if the normal temperature of the pond is remarkably low on the hatching days, and the pond is ice-covered during the night, and the water only a few degrees above zero during the day, the temperature may very well in bright sunshine, especially on the sloping sides with a southern exposure and where the bottom is dark, rise to 12°—15° C., or even more; the hatching temperature for the eggs therefore lies much higher than a mere cursory examination would make one suppose.

11. The females deriving from the resting-eggs are always amictic ones, but it may be shown that very soon, most probably already in the second generation, the mictic females appear. Knowing that the life of the males is only a few days, and finding the males in Nature at an air-temperature of a few degrees above zero as in December and March, it will be understood that even if thin-shelled eggs are deposited at the above-mentioned rather high temperature, they may on the other hand also be able to endure a low temperature and still be hatched.

12. Since we find the males in December as well as in March at temperatures about zero and in May when the temperature in the ponds may rise to about  $20^{\circ}$ – $22^{\circ}$  C., it is highly improbable that the temperature itself should have any direct influence on the production of the mictic females, at all events it can only influence the rate at which the male eggs are deposited and developed.

13. It is of course quite impossible from an investigation carried out in Nature to form any valuable ideas with regard to those factors which may determine the development of the mictic females.

It can only be maintained that the life of the colony in the active stages is founded by the amictic females, and is completed by the mictic ones. The preponderance of thin-shelled eggs in the first period, and the occurrence of resting-eggs only in the last, showed this conspicuously.

The life of *Hydatina* shows conspicuously that the purpose of the amictic females is in the shortest possible time to augment the number of the mictic ones; from a biological point of view they are to be compared with the sporocysts and redias among the Trematoda whose main task it is to develop the enormous amount of that larva material (the Cercaria) which is later on to develop into the ripe Trematoda.

14. A special characteristic of the *Hydatina* colony is that they die out entirely when the resting-eggs are laid. Among most of the other Rotifera some of the amictic females continue the propagation for months or often almost the whole year round, producing, after the death of the mictic females and males, a long series of amictic generations, whose propagation, however, as a rule seems to be very restricted, giving rise to those single individuals, which may be found the whole summer after the extinction of the great spring maxima, ending in the well-marked sexual period.

15. That these amictic females of the *Hydatina* do not, however, entirely disappear in all localities when the active life of the colony stops has been shown by this investigation, and also by other investigations in other parts of the world. We have seen that in permanent ponds *Hydatina* may now and then be found as a semipelagic organism throughout the summer months. The number is always very or rather small, and sexual periods have never been observed. Nor has it ever been seen that these amictic females, as is the case with other Rotifera, have begun a new and stronger propagation in the autumn, giving rise to the development of mictic females, the production of males and the deposition of resting-eggs,

i. e. an autumnal sexual period, or in other words a dicyclic propagation. Everything would seem to show that *Hydatina* is a pronounced monocyclic rotifer with a very short active lifetime in early spring, and in most localities without the development of amictic females, which are able to form a transition to an autumnal sexual period. It seems highly probable that the mictic females appear already in the second generation, most probably from the last laid eggs. That the temperature and variations in the chemical composition of the water may in reality exert their influence and accelerate or retard the development of the mictic females is probable. On the other hand, it must not be forgotten that, in the very short time the colony lives, it is rather improbable that variations in outer conditions would alone be able to cause their appearance. The total extinction of the whole colony when the resting-eggs are laid, seems to contradict this. It is as if the life of the colony is exhausted with the formation of resting-eggs, even if external conditions would allow life in active form.

### **Rhinops vitrea** Hudson.

Plate I, fig. 1—2; Plate V, fig. 3—5.

During my explorations I fairly often found *Rhinops vitrea*; in a few cases it occurred together with *Hydatina senta*; this was the case in the Fredensborg Castle Pond. It was, however, never like this species found in ponds which got liquid manure in such quantities that the water was coloured yellowish; furthermore it has never been found in ponds which were totally desiccated during the summer. It seems as if its home is mainly in small ponds, either without vegetation or at all events with a conspicuous central part free from vegetation. Its foot glands are not so large as those of *Hydatina*, and the secretions do not play so great a rôle in the life of the animals as those of *Hydatina*. In accordance with this it is not like *Hydatina* a creeping animal, and has no affinity to the surface film. It is a pronounced but rather slow swimmer. In contradistinction to *Hydatina* the amictic females produce young ones, whereas the offspring of the mictic ones, if fertilised, are very beautiful large resting-eggs. As far as I know, every female only produces one single egg; this egg I have never seen laid; on the other hand I have very often found empty skins of *Rhinops* with a large resting egg inside. I am therefore inclined to suppose that these eggs are not liberated before the mother organism decays.

Owing to the different offspring the two females, the amictic and the mictic, can always easily be distinguished from each other. The first-named if unfertilised almost always carry two or three young ones, the mictic if unfertilised 7 or 8 eggs or young ones in different developmental stages, and, if fertilised, the large resting-egg (Tab. V, Fig. 3—5). At the moment of birth the young one is pushed out in the course of a second, and if it is an amictic female, has at birth  $\frac{3}{4}$  of the size of the mother organism, if a mictic one only  $\frac{1}{3}$ , though later on it attains a size

of about  $\frac{1}{2}$ ; the very old males are still larger, very slow and very hyaline. Already at birth the amictic females carry well-developed eggs.

Asminderød Pond. *Rhinops vitrea* is a pronounced spring form. In 1922 it appeared immediately after the ice had disappeared. It has its large maximum already in April at a temperature of  $8^{\circ}$ — $10^{\circ}$  C., the maximum lasts the whole of April; in the beginning only large amictic females appear, these produce a large amount of brood, which immediately after the birth begin parthenogenetic propagation.

About 20/IV the mictic females appear, and in the plancton the males are now numerous. In the last week of April almost all females carry resting-eggs. The mictic females are still numerous; on 30/IV *Rhinops* is very rare and already by 9/V not a single specimen can be found; in all samples from 9/V to 4/XII it was totally absent; during this time the species only existed as resting-eggs. On 4/XII a few specimens of amictic females were observed; the pond was ice-covered in the latter part of December, and when it was again open in 1923 (24/III) *Rhinops* was fairly common; most probably it had a maximum during the time 24/III—10/IV; already at that time mictic females with resting-eggs are found. From May 1923 and through the whole of 1924 *Rhinops* almost entirely disappears; it was only found in a few specimens on 1/V 1924; the pond had been ice-covered till 15/IV. In the following years the pond became part of a villa garden and was very much altered; no samples could be taken.

Fredensborg Pond. The species is found in a few specimens on 10/IV 22, the last specimens are seen on 31/V. During the period 15/IV to 30/IV males are common. In the samples 11/V to 17/V most of the females carry resting-eggs; after 31/V not a single specimen has been observed. During 1923 *Rhinops vitrea* was observed sporadically in a few spring-samples. During the years 1924—29 the pond grew year by year more dirty and not a single specimen was observed.

*Rhinops* was most thoroughly studied in 1927 in the so-called Spejldam (mirror pond) in the Royal Garden of Frederiksborg Castle.

Till 7/II all ponds have been open almost the whole of the winter; the temperature of the water during the whole of the winter was between  $3^{\circ}$ — $5^{\circ}$  C. On 1/II a few amictic females were found. From 7/II to 16/II the pond was ice-covered, but with a small border of water near the shore. Here *Rhinops* was found on 7/II and on 16/II. During the period 16/II to 7/IV *Rhinops* was found on 28/II, 1/III, 15/III, 24/III, 1/IV and 5/IV; it was rather rare and always present only as amictic females. During the whole period the temperature of the water was not above  $8^{\circ}$  C., and very often  $4^{\circ}$ — $5^{\circ}$  C., the pond being often ice-covered during the night. Then rather suddenly the maximum set in on 7/IV; during the week 7/IV—14/IV it was very high; the large females often carry (7/IV) two or three large young ones which, when born are  $\frac{2}{3}$  of the size of the mother; the process of birth is observed; it takes place in the fraction of a second. In the same week mictic females are very numerous, and on 14/IV almost all females carry the large,



spiny black resting-egg. A female seems never to produce more than one single egg. During the days 15/IV to 20/IV the species disappears. On 20/IV only a few females were found. The temperature of the water was between  $5^{\circ}$ — $8^{\circ}$  C. during the period 7/IV to 20/IV. Very often specimens were isolated and fed with minute algæ; the cultures always died and I am therefore unable to give any account of the number of young ones etc.

1. The result of the investigation seems to be that *Rhinops*, just like *Hydatina*, is a pronounced spring-form, with a very short active period, living the greater part of its life as a resting-egg.

2. The active period is in early spring, the resting-eggs being hatched immediately after the ice has melted.

3. As *Rhinops* lives in ponds which as a rule are never desiccated, it is very remarkable that it entirely disappears at a very early time of the year, at a water-temperature of about  $10^{\circ}$ — $17^{\circ}$  C., just when the water begins to teem with food. Furthermore it is of interest that, in a good many cases, amictic females may be found all the summer, always in rather small number, and that during that time mictic ones neither appear nor produce maxima with sexual periods in the autumn. This seems to show that, in this species, the active period and the production of mictic females is in the first place independent of those variations in the external medium which the species commonly meet with; if variations produced under quite unnatural conditions (in the laboratory) or such as it never meets with in Nature are able to influence the length of the active period and the production of mictic females is another question.

In Nature *Rhinops* will commonly only be able to produce about 5—6 amictic generations; the life of the amictic females does not last more than about eight to ten days, and that of the mictic females is most probably shorter.

4. The resting-eggs may be hatched at very low temperatures and the propagation of the amictic females takes place at temperatures only a few degrees above zero. —

## Brachionidæ.

### Brachinionus.

In my area of investigation I have been able to distinguish four well-marked species, which may also be regarded as "Formenkreise" viz. *B. pala* Ehrbg., *B. angularis* Gosse, *B. urceolaris* O. F. M., *B. Bakeri* O. F. M.

It has often been pointed out that the home of most of the *Brachionus*-species is chiefly the central part of small ponds free from vegetation (ZACHARIAS 1898 p. 114, SACHSE 1912 p. 68). This is the case with *B. pala* and *B. angularis*, which together with longispinous Daphnias and species of the genus *Ceriodaphnia* play a prominent part in the pond plancton; the other two species belong to the vegetation zone and are often found in ponds quite covered with vegetation, (with us

especially *Potamogeton natans*; with regard to *B. urceolaris* var. *rubens* see later. All the species are found in village-ponds of a pronounced eutrophic character, as well as in moors and tarns with yellowish and very clear water; this applies especially to *B. pala* and *B. angularis*. As these two species are present almost in all our ponds, it is no wonder that they are found almost in all the experimental ponds.

Both species, especially *B. angularis*, have occasionally adapted themselves to life in the pelagic region of smaller lakes. —

### **Br. pala** Ehrbg.

Plate V, fig. 9—30. Plate VI, fig. 1—5.

Frederiksborg Castle Lake. *B. pala* is one of the main forms of the rotifer plancton of the lake. Most probably it will be present in all samples, though it always seems to be very rare from the first part of June to the first of October. During the autumn it is only present in very small number; however, when winter comes, it is one of the chief forms in the plancton and this is the case whether or not the lake is ice-covered. A maximum may develop below the ice as well as in years when the lake is hardly ice-covered at all. This maximum is only developed by amictic females, which, curiously enough, are able to develop a rather conspicuous maximum at temperatures near zero. Consequently, when the ice disappears, very often *B. pala* is one of the main forms in the plancton. During the rising temperatures, especially when the temperature has reached about 10°—14° C., i. e. in the latter part of April, the enormous maximum sets in, and for a fortnight the water is filled with innumerable masses of *B. pala*. Because all *Brachionidae*, except *Notus quadricornis* Ehrbg., carry their eggs and the three kinds of eggs differ very much from each other (Tab. V, Fig. 24—26) it is easy to distinguish the two kinds of females from each other. It may therefore easily be shown that all females before the middle of April are almost exclusively amictic ones, carrying two or three large eggs; a few mictic females with a cluster of as much as 10—15 male eggs occur. Then comes a moment when the mictic females preponderate over the amictic ones. Shortly afterwards (about 1/V) the mictic females carry a few, (one or two) large brown rather irregular resting-eggs. In the latter part of April and especially during the first half of May countless numbers of resting-eggs are deposited on the surface, whence the wind sweeps them to the edge and into the bays of the lake. If a milky glass disk is placed directly under the surface, only covered with a few centimetres of water, countless numbers of small black points, the resting-eggs, are observed. Shortly afterwards *B. pala* almost entirely disappears from the plancton of the lake; but nevertheless through the rest of the year single individuals occasionally appear; but these singletons are always amictic females.

When autumn comes, the strong gales sometimes carry masses of resting-eggs, deposited along the edges, out on to the lake. About 1—2 weeks later *B. pala* is

more common. These females, all amictic ones, are very large, very hyaline and all without thorns; it is these forms which form the slowly increasing maximum of the winter.

These large females have no thorns when born; most probably they do not get them later; a little later, in samples often taken below the ice, other large females with short thorns, (forma *amphiceros*) appear; all these large females with thorns or without thorns predominate in the first part of April; in the latter part and in the beginning of May forms occur which are only half as large; they have no thorns and all carry clusters of male eggs, i. e. they are the mictic females. At first it would seem as if we had here a conspicuous morphological difference between the two kinds of females. But already eight days later the samples show every possible intermediate stage between them: large forms with thorns and male eggs, and with thorns and amictic eggs; furthermore large forms with thorns and resting-eggs. The two kinds of females are no more morphologically distinguishable from each other; only one form is never found; a small form with resting-eggs; there is no morphological difference between the two forms.

It seems as if the forma *amphiceros* may appear at all seasons and that its appearance is quite independent of temperatures and all variations in external conditions dependent upon this factor. All that can be said is that the mictic females are presumably born at an earlier stage than the amictic females; that the mictic females begin the production of eggs immediately after birth and grow stronger than the amictic females. It seems however that they only rarely reach the largest size of the amictic females. Most probably a more thorough examination would show a difference in size between an egg which produces a mictic female and one which produces an amictic one.

During the severe winter of 1928—29 *B. pala* and *B. angularis* were found in great number in openings in the ice; all were amictic females. When the ice disappeared, the species were extremely rare and the maximum and sexual period did not develop before the middle of May, about three weeks later than usual.

Asminderød Pond. *B. pala* always seems to have a very pronounced spring maximum which finishes with a sexual period. In 1922 the spring maximum did not begin until 15/V at a temperature of 15°—18° C., on the other hand, it lasted almost the whole of June. In 1923 and 1924 it began about 15/IV and was at its height about 15/V. The form was mostly without thorns otherwise the species was hardly ever found in 1923 and 1924 and, if so, only in a few specimens in a few samples; on the other hand, in 1922 it had a rather high maximum in August. This maximum was formed of rather small individuals, all carrying long posterior thorns. The maximum terminates in a sexual period; the mictic as well as the amictic females carry thorns.

Fredensborg Pond. Here *B. pala* is the main form of the rotifers. During the whole of 1922 from 25/IV to about 6/IX it was very common in all the samples. From 16/VII to 31/VIII it had a large maximum with a pronounced sexual

period. It disappeared from the pond during the latter part of September, and was not found again before May 1923. In this year, too, the great maximum did not occur until 16/VII and lasted to 20/IX whereupon the species only occurred sporadically in a few samples. In the latter part of July and during the first part of August the mictic females carried 16—20 male eggs, a little later often two resting-eggs. The amictic ones often carry four eggs in July; in August commonly only 1—2. The sexual period terminates in the latter part of August, but the amictic females have their maximum during the whole of September. In the latter part of this month many barren females appear. The main form of the pond is the forma *amphiceros*, but the length of the thorns varies enormously and is not associated with a special form of females.

Island Pond. Here *B. pala* is only found in a few specimens in a few spring samples; it does not belong to the plancton of the pond and is most probably introduced in the pond with affluxes.

The Horseshoe Pond. The occurrence here is very remarkable; it is lacking in most of the samples. In 1923 it appears rather suddenly in August and in November has a fairly large maximum. A new very small one appears in May 1924; most probably the species has not been present all the winter below the ice. Then it disappears again and is almost wanting till June 1925, when it has again a rather well-developed maximum; it never belongs to the main forms of the pond. A most peculiar fact is that in my numerous samples I have never found mictic females, never seen females either with male or with resting-eggs. If investigations abroad should give evidence of *B. pala* being amictic over a period of several years, it must be remembered that this has most probably been observed before. *B. pala* appears in the pond as the typical form; thorns are not developed at all, or at all events only to a very slight degree. —

Nøddebo Pond. *B. pala* was only found in May—June 1922 and in October 1924, always in a few samples, always amictic and always without posterior thorns.

Schæffergaard Pond. The species occurs almost in all samples, but only in small number; specimens with long thorns as well as without thorns occur. No mictic females have been observed.

As mentioned above, *Brachionus pala* is found in numerous ponds. When on a motor-car trip in the summer through the northern and middle parts of Seeland some 20 samples were collected from different ponds *B. pala* was found in most of them. In some of them the normal *B. pala* was found, in others the forma *amphiceros*, and then with posterior thorns of very different length. All attempts to connect the length of thorns with the habitat or external conditions are, as far as I can see, quite fruitless. A connection between them and pH, temperature and amount of food does not exist. Only one thing seems to be certain: the very long-thorned forms only occur at the highest summer temperatures. For a long time some forms found in Fjenneslev Pond mentioned pag. 116 had the longest posterior thorns

hitherto observed. The pond was so far from my home that regular observations could not be obtained. Later on in a little pond in the village of Bistrup on the shore of the Furesø a form was accidentally found on 22/VII 1929, with posterior thorns exceeding all that, as far as I know, has hitherto been observed. From 22/VII 1929 to August 1930 the pond has been under regular observation. On 22/VII 29 the species was one of the main forms in the plancton and extremely common, already by 2/VIII the number had diminished, and by 22/VIII it was rare. During September it was only present in very few specimens, and then it totally disappeared in all samples from October to May. From July to October the samples were taken every eighth or tenth day, later on in the year every fortnight. The species was in a sexual period on 22/VII, and this lasted till the middle of August whereupon the minimum set in. With regard to the investigations in 1930 see postscript.

During July (Tab. V, fig. 9—30) and the first part of August the long-thorned forms were present only, or mainly, and these were still found on 22/VIII, but then the thorns were shorter and the whole form smaller. Already on 2/VIII a very few forms shaped like a typical *amphiceros* with rounded posterior edges and short posterior thorns appeared; their number had increased on 22/VIII, and from the first days of September the typical *pala* predominated; during the latter part of September the species was only present in this form, and as such it disappeared from the plancton. These forms had no posterior thorns at all; they were of the typical *pala* form. Simultaneously with the loss of thorns they diminished in size; being almost only half the size they were in the summer. I am inclined to think that these forms derive from resting-eggs hatched too early.

The large thorned forms are mainly characterized by their enormously long, faintly curved, posterior thorns. The drawings were made from samples preserved in formaline and all characterized by the same position of the posterior thorns extended perpendicularly from the sides. In a sample taken into the laboratory in the living state, I saw to my great astonishment that during swimming the posterior thorns were stretched backward, lying parallel with the longitudinal axis of the body. Only at the moment when the direction was to be changed or when the wheel-organ, on striking against some object, was drawn in, the posterior thorns were suddenly thrown outward. As no muscles are attached to or enter the thorns, this may only be due to the pressure of the liquid in the body cavity when the wheel-organ is retracted. The observation may have some interest because it may contribute to show the significance of the thorns. When stretched backwards, they do not augment the cross-section resistance. And perhaps this is unnecessary during the swimming action. On the other hand, when the wheel-organ is retracted the motion is stopped, and at the same moment the posterior thorns are automatically thrown outward. It will be understood that, when the wheel-organ is withdrawn, they must, in a very high degree, contribute to augment the cross-section resistance. The development of the thorns goes hand in hand with augmentation in size; locally and temporally forms with strong thorns are larger and more robust

than those without thorns. It is a very peculiar sight to see these long-thorned forms, swimming round with the thorns stretched backwards, the moment a drop of formaline is added to the water suddenly, simultaneously with the retraction of the wheel-organ, throw the posterior thorns outward, and then die with the thorns in this position.

In the above named little pond at the village of Fjenneslev in the middle of Seeland a very peculiar *B. pala* form with very long posterior thorns was found in 1923. The pond is extremely shallow, having no more than 2—4 dm. of water. The water is filled with enormous amounts of grey decaying mud always stirred up by the numerous ducks and geese. Also the Daphnias: *Moina rectirostris* and *Daphnia Atkinsonii* are present.

In 1925 the pond was under the observation of my assistant Mr. BERG, who has kindly furnished me with some samples.

The periodicity of *B. pala* is here as follows:

1929	5/V	15/V	3/VI	9/VI	15/VI	7/VII	15/VII	25/VIII	31/VIII	7/IX	4/X	3/XI	18/V	1930
	0	0	0	0	0	+	c	cc	cc	v	0	0	0	

It is very regrettable that we have no samples from 15/VII—25/VIII. *Brachionus pala* did not appear before 7/VII, it was common by 15/VII and present in enormous quantities in the latter part of August. Then it rapidly diminished in number at the beginning of September and was not found later on in the year.

When it appeared on 7/VII it was as a typical small *B. pala*; when a sample was taken on 25/VIII, it was as forma *amphiceros* with much elongated and elegantly curved posterior thorns; only this form was present on 31/VIII. On 7/IX some specimens of this form occurred, but it was smaller and the thorns were not so long; simultaneously the forms appeared which we have met with on 7/VII, the typical *pala*. The whole development does not take more than about two months; the maximum at all events not more than 1½ months. During this period the form is extremely altered; it is hatched from the resting-egg as forma *pala*, but in the time 15/VII—25/VIII it is changed into *amphiceros*. As such the colony dies out; the few specimens found as forma *pala* most probably belong to material hatched from resting-eggs.

Far away from home it was impossible to me to get a regular series of observations for a whole year, but in the summer of 1929 I had as mentioned above the good fortune to find the same form in the above named little pond at Bistrup only about 14 kilom. from my home; here the observations were completed and the results discussed in the postscript.

*Brachionus pala* forma nova.

Plate VI, fig. 2.

In a small pond near my summer laboratory at Tjustrup Lake I found, on 1/VIII 29, a very peculiar *Brachionus* (figured plate VI, fig. 2). It was very small, shaped like *B. pala* and had no thorns. It immediately attracted my attention owing to its enormous resting egg, almost half as large as the animal. It was very dark

and covered with a coating of short dark spines. A coating of this kind is unknown on the resting-eggs of other *Brachionus* species; that of *B. pala* has nothing of the kind; the dark surface is smooth, only with fine punctures, but as far as I know, never with spines. The animal was furthermore characteristic by the enormous mastax and very strong mouth-parts with the manubria of another form than those of *pala* and, as far as I could see, with more teeth in the unci. The wheel-organ was of the normal structure, but the bristles on the lobes unusually strong; the number of cells in the stomach was much larger. The species had an enormous maximum which persisted till about 15/VIII, at that time the pond was slowly desiccated, having only 1 dcm. of water. In the last days of August the pond had no water at all. As long as the young ones hatched from the resting-eggs are unknown, I will not venture to create a new species. For comparison a *Brachionus pala* forma typica from Frederiksborg Castle Lake is drawn with the same power as the new form from the little pond at Tjustrup lake.

Of all the *Brachionus* species *B. pala* is, at all events in my country, that which is best able to live a pelagic life in fresh-waters which may with some right be regarded as lakes, at all events as pond-lakes. This holds good especially for fresh-waters which contain huge *Cyanophyceae maxima*. It has, for instance in Viborg Lake (about 300 ha. large and with a depth of about 15—16 metres but with high *Cyanophyceae maxima* during the summer), a very high spring maximum with a well developed sexual period in May, in the other samples it occurs only in rather a small number.

Even if *B. pala* does not occur regularly in the pelagic region of the larger lakes, it is fairly often found in the bays, especially where these are well separated from the main lake; from them gales may occasionally carry some specimens across the lake into the real pelagic region, where the species is not however, as far as we hitherto know, able to keep its place.

### ***Brachionus angularis* Gosse.**

Plate V, fig. 6—8.

Frederiksborg Castle Lake. *B. angularis* most probably occurs singly the whole year round. In late autumn and during winter it is, with *B. pala*, the main form of rotifer life. This is the case whether or not the lake is ice-covered. The maximum develops below the ice and when the lake gets ice-free it is the main form of all rotifers in the lake. The great maximum begins at a temperature of 10°—12° C., and simultaneously the mictic females appear. In the latter part of May the resting-eggs are formed; with those of *B. pala* they are deposited in countless numbers on the surface. Then the species almost disappears; but some specimens are always present; whereas *B. pala* does not reappear before late autumn, *B. angularis* may have a fresh but slighter maximum in August, which terminates in a well-marked

sexual period; then it gets rarer again, again increasing in number in the latter part of November.

As is generally known, *B. angularis* has no thorns at all, but a peculiar feature of this summer-form in Frederiksborg Castle Lake and elsewhere is the very thick and very conspicuous gelatinous envelope surrounding it. Moreover, in this summer-form the posterior lateral organs are placed on a pair of processes which gives the animal a peculiar posteriorly angular appearance. The long lateral organs protrude through the envelope. The form is amictic as well as mictic; it disappears in the first part of September; in the latter part of November the new form without an envelope appears.

Asminderød Pond. *B. angularis* is beyond doubt perennial. There is a pronounced maximum in May and this maximum was observed in all the three years of observation; it always terminated in a sexual period and then the species almost disappeared. During this summer minimum all specimens were amictic females; and from June to April—May next year mictic females were never observed. In 1922 and 1924 but not in 1923 a slight maximum was observed in July—August; but no mictic females were observed. In this pond the above-named gelatinous coating was not seen.

Fredensborg Pond. *B. angularis* appears in the sample 10/IV 1922 and has then a large maximum in June, followed by a sexual period; most probably it is perennial, amictic females being present the whole year round; in 1923 the spring maximum was small.

Island Pond. During the years 1922—1924 *B. angularis* was most probably perennial, but it was almost always present in small number and often absent in a good many of the samples. In 1922 a maximum followed by a sexual period was observed in the autumn.

Horseshoe Pond. In May 1923 *B. angularis* had a conspicuous maximum followed by a sexual period; then it almost disappeared from the plankton, occurring with only a few amictic females during the rest of the year. This was also the case almost the whole of 1924. Then suddenly in November a very high maximum appeared and this lasted the whole winter; this maximum, however, was only formed by amictic females; no sexual period was observed. The form is very large, very hyaline and differs somewhat from the typical *B. angularis*.

Nøddebo Pond. During May and June *B. angularis* was present but always in small number; the greatest number occurred on 24/V 24. Only amictic females were observed.

Schæffergaard Pond. *B. angularis* is most probably perennial. It was observed almost in all samples. During November—March it had rather a large maximum which terminated in a sexual period, the mictic females appearing very early in the latter part of March. During the rest of the year only amictic females were observed. The species in Schæffergaard Pond has a rather peculiar appearance, the carapace being covered with a rough coat which gives it a brownish aspect. Similar specimens have been observed by others.



It is almost impossible to take samples from any of our ponds without getting *B. angularis*; maxima may be found at almost all seasons of the year; it is often one of the main forms in plancton samples from November and during the whole winter. Sexual periods are for the most part observed in spring; during the rest of the year only amictic females seem to occur.

Now and then it may also occur in rather large ponds and small lakes, or in the pelagic regions of larger lakes into which the specimens are carried from the littoral region and from small bays. It may have very large maxima, especially in eutrophic ponds, village ponds, duck ponds etc., but on the other hand it is by no means rare in peaty water. Especially in lake ponds covered with Cyanophyceae (*Microcystis*, *Anabaena* a. o.). *B. angularis* may be rather common in the pelagic region. This is, however, due to the fact that they sit on the Cyanophyceae colonies, using these as a substratum quite like various species of *Vorticellidae* and *Chydorus* which are found in company with them. There is therefore some truth in LEMMERMANN'S statement (1898 a. p. 183) that the *Brachionus* species are pelagic in the Cyanophyceae lakes but littoral in the Flagellata lakes.

#### ***Brachionus urceolaris* O. F. Müller.**

Frederiksborg Castle Pond. The species is no real plancton organism. During the whole winter, the rootlets from the chestnut trees hanging down into the water are covered with a coating of *B. urceolaris* and species of the Fam. *Philodinidae*. They give the rootlets a reddish shaggy appearance. Especially in April 20/IV—1923 the species had an enormous maximum, colouring the water reddish in the littoral zone round the chestnut trees. Simultaneously mictic females appeared, and if now material was taken into the laboratory, crowds of males gathered in the lighted border of the vessels; a week later almost all females carried resting-eggs. Then the species totally disappeared and was not observed again until late autumn. Just when the maximum is at its height, strong winds may carry shore material out over the lake, and *B. urceolaris* may then for a short time appear to be rather common in the pelagic region. The whole phenomenon only lasts a very short time. With these observations in mind, it is no wonder that *B. urceolaris* is often found in single specimens in central parts of ponds and smaller lakes, this is the case e. g. in Asminderød Pond and Horseshoe Pond, and in many ponds scattered over the whole country. Everywhere the occurrence is sporadical; a more thorough study would most probably reveal the place of origin of the animals.

Nøddebo Pond. Especially during the summer months this pond contains a regular porridge of *D. pulex* and *D. longispina*. Chiefly during May—July the *Daphnias* are covered with a coating of reddish *Brachionus*, unquestionably *B. rubens* Ehrenberg, nowadays regarded merely as a variety of *B. urceolaris*. When the *Daphnia* moult, the *Brachionus* are thrown off with the coatings, and therefore some specimens are always free-swimmers, whereupon they very soon again fasten

on to other individuals. A sexual period was observed in June—July, and during that period it is a rather pleasant sight to see twenty to twenty-five males encircling a *Daphnia* covered with *Brachionus* specimens. The phenomenon lasts till about September—October, then the species seems totally to disappear; the species seems only to hibernate as resting-eggs. In another pond in the village of Bistrup near Furesø the *Daphnias* were under observation the whole summer of 1929; *B. urceolaris* var. *rubens* appeared on the *Daphnias* in August and suddenly in September had an enormous maximum with crowds of males and countless masses of resting-eggs. All *Daphnias* were wrapped in coatings of *Brachionus* but the plancton itself was almost exclusively formed of *B. urceolaris*.

### B. Bakeri O. F. M.

*B. Bakeri* is a common species during the summer months often met with in small ponds covered with vegetation. It has never been found in the central part of ponds, and is never plancton-building like *B. pala* and *B. angularis*. As is generally known, especially through the investigations of ROUSSELET, it is an extremely varying organism. Mictic females with male or resting-eggs have often been found, but always in very few specimens. The sexual period occurs at rather high temperatures. During the winter months the species seems commonly to disappear totally, most probably hibernating almost exclusively as resting-eggs. During the very mild winter 1929—1930 in which the ponds were open the whole of January *B. Bakeri* in the form of *B. quadratus* had a large maximum in the little pond in the village of Staunstrup near the borders of Furesø. The maximum began in the first days of January at a temperature of 3° but before February almost at the same temperature the species had totally disappeared. Simultaneously enormous amounts of *Cyclops-nauplii* were developed. Only amictic females were observed.

Without any more thorough investigation I have received the impression, that the numerous greatly differing forms are locally not temporally separated forms. They are not seasonal variations; but every pond seems to have its own race fairly fixed in form, whose variations seem to be rather limited. A more thorough investigation would be desirable.

If now we try to sum up what has been gathered from this investigation with regard to the biology and especially the propagation of the *Brachionus* species, we arrive at the following results.

1. The *Brachionus* species belong in the first place to small shallow ponds, more or less covered with vegetation; apart from *B. Bakeri* which prefers ponds with clear often peaty water, they frequently live in ponds rich in organic matter. Two of the species, *B. pala* and *angularis*, are true plancton organisms in the central parts of ponds and smaller lakes, and may occasionally be found in the pelagic region of rather large pond-lakes, especially those which have high Cyanophyceae maxima.

2. Because the genus *Brachionus* as well as related genera and *Anuraea* carry their eggs in the posterior part of the body and these eggs, the female eggs, the male eggs and the resting-eggs, all differ from each other, it is always easy to distinguish the amictic and mictic females by means of the eggs. In these species, therefore, it is easy to ascertain the occurrence of mictic females.

3. It may then be shown that mictic females occur only in a very few months of the year, often only for a few weeks; specimens which are found beyond these periods are almost always amictic. In some localities and in some years, also, the amictic females totally disappear, the organism then living for months only as a resting-egg; but very often after the great maxima and after the disappearance of the mictic females, some few amictic ones remain in the water layers, having for months only a very slow propagation.

Now and then the propagation of these amictic females (apart from the sexual periods) may increase, causing rather large maxima, especially in the autumn and at the beginning of the winter. It seems as if these maxima only rarely terminate with the appearance of mictic females and a sexual period. During winter, and especially below the ice, only amictic females occur.

In spring, commonly at temperatures about 10° C., the amictic females begin the propagation of mictic ones and a conspicuous sexual period almost always occurs in the spring. Having deposited the resting-eggs, the mictic females again disappear, and the maximum is at an end.

Apart from this almost always very conspicuous spring maximum followed by a sexual period, a second maximum with a sexual period may occur in August—September; occasionally a maximum was only observed in the autumn.

In some colonies (*B. angularis*, Frederiksborg Castle Lake) the maximum and the sexual period may develop in spring at a temperature of 14° C. and then again at the highest temperature in August. In Schäffergaard Pond there is a spring maximum and then another beginning in November; it is large in winter at temperatures round zero and there is a sexual period in March.

In reality the life of the species differs from pond to pond.

SACHSE (1912 p. 77) has arrived at a similar result. He maintains that between the two pronounced maxima the species have what he calls "Nebenmaxima", and he tries to connect all these maxima with the curve for the centrifuge plancton.

Heavy showers may almost quite suddenly kill a whole maximum, but on the other hand, when they fill the desiccating ponds again and the resting-eggs develop, sudden maxima may appear.

It seems as if the "Nebenmaxima" are more pronounced towards the south.

4. With regard to the formation of resting-eggs and their future fate the following observations may be added. The amictic female of a *Brachionus* e. g. *B. angularis* (Tab. VI, fig. 6—10) carries a rather light round or faintly band-formed vitellarium with eight conspicuous nuclei. It carries simultaneously one to three light

thin-shelled eggs. In the mictic female carrying male eggs the vitellarium has often one part much darker than the other, and this part is crowded with oil globules, often of a bluish colour. The number of the small male eggs is often 4—6. Many mictic females carry no eggs but the whole vitellarium is altered into a dark mass crowded with oil globules and in which nuclei are not visible. Isolated, these females will in the course of a few days have formed a single large resting-egg, thick-shelled and surrounded by the rest of the vitellarium. A little later the female carries one or two resting-eggs; they may be irregular of form and often differ somewhat in aspect. In the youngest of them the egg presents itself only as a dark resting-egg with homogeneous contents, in the others the contents have formed a globule placed centrally and with great spaces between it and the wall; the vitellarium is now much smaller. How many resting-eggs the females produce we do not know, but probably their number is not large. It seems as if the eggs are carried rather long; when carried by the mother animals they show no differentiation as far as I can see; only a circumpolar furrow at one of the poles is conspicuous. When thrown off the eggs rise to the surface; when found there, the development has begun, and between the egg and eggshell air has been developed (Tab. VI, Fig. 3—5). In this stage the eggs may be frozen into the ice or thrown up on dry land. In the spring the development of the embryo goes on again and the air is now pressed in the shape of a sausage into the posterior part of the shell. At the end of the development the embryo is lying in a very thin membrane with the wheel-organ working against that part of the shell which is bounded by the above-mentioned furrow. The result is that the part lying above the furrow comes off like a lid, and the embryo, bursting the membrane, is liberated and swims away. In the shell remains of the membrane are found besides the large air globule which makes the empty shells float the whole year round on the surface of our lakes. Most of the material of autumnal resting-eggs will be carried by gales into windsheltered creeks and together with ephippia of Daphnids form the grey mosaic ice characteristic of localities of this kind. On the northern exposed coasts the temperature in early spring will in bright sunshine rise to 7—10° C. even if the lake is still ice-covered. On account of these high temperatures the development of the hibernating organs is accelerated and on the first days of spring, just when the ice has disappeared, the newly hatched material forms milky clouds in creeks with a northern exposure. From here the clouds of plancton organisms spread over the pelagic region of the lakes and the huge maxima set in.

5. As is generally known, some of the species, especially *B. pala* and *B. Bakeri*, are subject to great variations. In reality we have to do with "Formenkreise", the one *B. pala-amphiceros*, the other *B. Bakeri-cluniorbicularis*. The first-named "Formenkreis" includes thornless forms (*B. pala*) transitional to forms with thorns of very different lengths (*B. amphiceros*) the other "Formenkreis" passes from forms with very long thorns (*B. Bakeri*) to forms without thorns and rounded posterior edges (*cluniorbicularis* Scoricow); intermediate stages are *B. brevispinus* Ehrbg. It is this "Formen-

kreis" which has been well illustrated by ROUSSELET (1897 p. 328). Later on it has been subjected to an experimental but hitherto only preliminary investigation by DE BEAUCHAMP (1924 p. 1207; 1924 p. 1290).

As far as I can see from my explorations in Nature, the variations are not confined to one of the two sorts of females; the mictic as well as the amictic ones may both occur with and without posterior thorns.

6. *B. pala* is one of our most common plancton rotifers in ponds and smaller lakes. Its size and appearance varies enormously from pond to pond; it may almost be said that every pond has its own race. Especially the length of the posterior thorns varies enormously; these are well known facts, corroborated by almost all observers. In different ponds and smaller lakes where *B. pala* disappeared as *amphiceros*, I have observed that it always appears next spring as *B. pala* without posterior thorns; moreover I have taken lots of resting-eggs, hatched them in my vessels, got swarms of individuals but never in the first generation seen a single one with thorns. — One thing, therefore, seems certain. The young ones hatched from resting-eggs seem always to be without thorns.

In some localities only thornless specimens occur; in others sooner or later thorned specimens combined with thornless ones or the first-named alone are present. The thorned forms appear suddenly, but it seems as if forms with very long thorns occur mainly at the highest temperatures. It would be of interest to clear up how these very longthorned colonies and those whose thorns are bent outward behave whether in this case, too, the specimens deriving from resting-eggs are thornless and if the length of the thorns increase with rising temperatures. —

With regard to my own explorations I refer the reader to the postscript of this work. — Here I only wish to remark that DE BEAUCHAMP relating to *B. Bakeri-cluniorbicularis* has arrived at the following main results "La variation des Brachions apparaît comme un phénomène des continu, sans doute déclanché par des facteurs, ou plutôt des variations de facteurs-externes, mais sans lien spécifique au moins avec ceux que j'ai pu expérimenté jus'qu'à présent et largement dépendants des facteurs internes, d'une fécondation qui paraît la fixer dans une certaine mesure. Elle aurait donc le caractère de mutation réversible plutôt que celui de fluctuation continue."

7. Investigations of living animals seem to show that the long thorns of *B. pala* may have significance by increasing the cross-section resistance. With regard to this point reference is made to page 115.

#### **Schizocerca diversicornis** Daday.

Asminderød Pond. *S. diversicornis* was a pronounced summer form through all three years of observation, appearing in a few specimens in the middle of May or in the first part of June; before November it had always entirely disappeared,

in 1922 already in the middle of October, the active life being restricted to about four summer months. The summer maximum is always small till the middle of July, then, at the highest summer temperature, the maximum may be so great (for instance in 1924), that *S. d.* is almost one of the main forms of the plancton. Until that time only amictic females with one or two eggs have appeared. Then rather suddenly the mictic forms with chains of three to four male eggs, not clusters as in *Brachionus*, appear; shortly afterwards the females with the dark oblong resting-eggs are found. Already in the latter part of August the species is rare.

Horseshoe Pond. *S. diversicornis* is very rare in all three years of observation, only a few individuals occurring in a few summer samples, always at highest summer temperature; it was common only on 29/VI; 16/VII 23; 31/VII 24 and at that time mictic females have also been pointed out.

*S. diversicornis* is not among the commonest of our Rotifera; in several ponds near Hillerød it has, however, been observed year after year. I have found it in ponds with thick Cyanophyceae maxima (*Coelosphaerium Kützingianum*) and in rather small village ponds with thick coatings of *Microcystis*.

It is everywhere a pronounced summer form with a maximum at the highest temperatures. In this short active life of the species the fairly large maxima are here as everywhere else due to the amictic females. In the last part of the maximum, when almost every female either carries male eggs or resting-eggs, it seems as if only mictic females are present. The period in which mictic females appear is restricted to a few weeks. Like other pronounced summer forms *S. diversicornis* has no active period of life caused by amictic females with decreasing fertility; when the mictic females disappear, the life of the colony is at an end in our latitudes. The species disappears from the plancton almost quite suddenly, at nearly the same temperature at which it appeared. The first specimens are commonly found on 17/V, the last on 18/X.

#### Noteus.

Of the three *Noteus* species I have, in Denmark, found *N. quadricornis* and *N. militaris*.

#### *N. quadricornis* Ehrbg.

In contradistinction to all hitherto known species of the family *Brachionidae* *N. quadricornis* is a pronounced bottom organism, blind, extremely slow, creeping over the decaying matter covering the bottom of small ponds.

It is by no means rare, but has hitherto never been found in great numbers; in every sample only one or a few specimens occur. I have never seen it carry its eggs; most probably they are deposited on the bottom. It seems as if it is most common at low temperatures; most of my finds belong to late autumn.

**Noteus militaris** Ehrbg.

I have only seen this rare animal a few times in a little pond upon Regnstrup Overdrev, near Tjustrup Lake. In contradistinction to *N. quadricornis* it is a free-swimming organism; when I found it, it was swimming freely among the leaves of *Potamogeton*. It has further been found in a village pond near Hørsholm on 22/VIII 1914. It seems to be a pronounced summer form; only amictic females have been observed.

**Anuræa.**

All *Anuræa* forms from my area of exploration may be referred to *A. aculeata* Ehrbg., *A. cochlearis* Gosse and *serrulata* Ehrbg. In my opinion *A. tecta* Gosse may be regarded as a distinct sub species.

**A. aculeata** Ehrbg.

Plate VII, fig. 1—47.

Frederiksborg Castle Lake (fig. 1—5). *A. aculeata* is perennial with a very pronounced spring maximum, which is commonly over before the first of June; it begins at very low temperatures; *A. a.* is present below the ice, but not in great number, during the whole of the winter, whereupon a maximum begins about 14 days after the lake is open. (Temperature 6° C.). During the winter of 1925, when the lake was open almost the whole year, it was the principal form in January and February at a temperature of 3°—5° C.; but the main maximum did not occur before the last part of April at a temperature of 12° C. Later on the species was always present, but always in a few specimens or a very small number.

A sexual period is always observed in May, as a termination to the large maximum. In 1923 mictic females appeared on 8/V, carrying chains of three to four male eggs, and again on 6/V 1924. The sexual period is really very short as is also the life of the mictic females; for a week almost all mictic females carry resting-eggs, in this lake always covered with a rough coat; in 1925 I did not observe the sexual period. Mictic females have never been found from the 1. of June to April next year.

The propagation of the amictic ones continues the whole year round after the end of the sexual period, but this propagation seems always to go on very slowly at high temperatures, proceeding more rapidly at lower ones. The maximum begins to develop at low temperatures in November and reaches a considerable height during the winter, especially when the lake is not icebound; this may not only be due to an acceleration of the propagation of the active material of the species, but also to individuals hatched from resting-eggs, perhaps especially from those which have for a short time been icebound and again set free.

In the course of the three years 1923—1925 *A. aculeata* showed a peculiar seasonal variation. During 1923 (Tab. VII, fig. 1) *A. aculeata* occurred with very

long posterior thorns, which in the latter part of May and June were curved much outwards. During November and December some individuals possessed thorns which were only half the length of the lorica. During the winter, in samples taken below the ice, until March, only forms with short thorns occurred; these forms predominate until the latter part of May (fig. 3—4) when again forms with thorns as long as the lorica rather suddenly appear (fig. 5). During the rest of 1924 only long-thorned specimens were present. In 1924 the sexual period was restricted to that part of the year when forms with short posterior thorns were present; in 1923 when only forms with long posterior thorns were present, these forms, too, carried male eggs as well as resting-eggs.

It seems as if *A. aculeata* in Frederiksborg Castle Lake has a two or three years' period during which the size of the posterior thorns is slightly diminished; if it is possible to regard the diminution as a sign of degeneration, the formation of resting-eggs would set in when it was at its height i. e. when we had to do with forma *brevispina*; the long-spined species, suddenly appearing in June, would then be hatched from the resting-eggs just formed.

Asminderød Pond. *A. aculeata*, presents very peculiar phenomena in Asminderød Pond. During the whole of 1922 it was very rare and was only observed as a typical *A. aculeata* (fig. 39—40). In 1923 a great maximum suddenly occurred in March and April; it was a small form and occurred mainly as forma *valga* (fig. 41—44) with one short and one long posterior thorn; in addition every possible transitional stage between *A. aculeata* f. *typica* and *A. aculeata valga* occurred. During this maximum the sexual period set in and the amictic as well as the mictic females presented all variations with regard to the length of the thorns. Forms with resting-eggs (covered with thorns) were numerous, especially in the latter part of April. But already on 6/V (fig. 42—44) most of the forms had the two posterior thorns of equal length, but rather small (fig. 45); on 25/V quite another form, very large, with both thorns equally long, was the principal form. At this time *valga* had disappeared and the sexual period was at an end (fig. 47). The large form was now the only one occurring in the plancton from June 1923 and to December 1924 (fig. 45—46), but during the whole of this period only a very few specimens were seen in each sample. A few *valga* appear again. In April 1924 the large form had no pronounced maximum and no sexual period, and all the animals had posterior thorns of equal length; it was rare from June 1923 to November 1924 when rather a small maximum set in, and when *valga* appeared again. Apparently a great part of the resting-eggs formed in 1923 had not developed during the last six months of 1923 and the whole of 1924.

Fredensborg Pond. In 1922 *A. aculeata* most probably occurred in all the samples; in August—September it had rather a large maximum, but after October and during the whole of 1923 it only occurred in a few samples. Already in May and June 1922 it occurred mainly as *valga* (fig. 15) but with a very great difference in the length of the posterior thorns. In the first part of September mictic



females appeared which carried short-thorned resting-eggs; all forms were short-thorned with equal length of the thorns or of forma *valga*.

When the sexual period was at an end, the species became extremely rare. When it reappeared in 1923 (fig. 16—18) it was much larger, and had now its typical form with two equally long posterior thorns.

Island Pond. *A. aculeata* is perennial with a pronounced spring maximum; after the latter part of May it almost always occurred in small number, and it seems as if the number increases somewhat in the autumn. During 1923 the species was a typical *A. aculeata* with two equally long posterior thorns; no sexual period was observed (fig. 19—20). On the other hand, in 1924, when the pond had become icefree, the species occurred in a very small form on 20/IV with very short thorns (fig. 21) and on 16/V the thorns had totally disappeared (fig. 22). Simultaneously a sexual period set in, and mictic females with chains of 3—4 male eggs or resting-eggs appeared. The resting-eggs had a smooth surface, and had no coating of short thorns. When the sexual period was at an end, the maximum ceased and the rather few specimens which occurred during the rest of 1924 and the whole of 1925 had all well-developed posterior thorns, which especially in August were curved outward (fig. 23). Curiously enough, during the whole of this time, I was unable to find any trace of a sexual period; apparently all females were amictic.

Horseshoe Pond. *A. aculeata* occurred in 1923 and in 1924 till November, but in very limited number; it was absent in many samples, and in most of them only found in small number. Then rather suddenly during the time 13/VI 24 to 16/II 1925 it had a rather large maximum, whereupon it again diminished in number. In the latter part of 1924 mictic females occurred, carrying three to four male eggs or smooth resting-eggs. Apart from the period with a maximum and sexual period, the species always had unusually long posterior thorns, and was furthermore peculiar owing to its great breadth (fig. 9—11). But during the maximum the species was short-thorned and these short-thorned forms (fig. 12—13), to which mictic as well as amictic females belong, were the main forms during the winter, and were still predominant in February; simultaneously long-thorned individuals occurred, and during the rest of 1925 all females belonged to that type (fig. 14). No sexual period was observed in 1925.

Nøddebo Pond. The occurrence of *A. aculeata* is very peculiar. In 1922 it had a large maximum in July; the maximum terminated in a sexual period; otherwise it is rare. It was almost absent or extremely rare during 1923 till September when it had a large maximum; then it almost totally disappeared and did not reappear before May—June 1924. During the rest of 1924 it was very common; in all the succeeding samples either *A. cochlearis* or *aculeata* was the predominant form.

When *A. aculeata* appeared on 4/VII 1922 it was as forma *brevispina* (fig. 24) and as such it had its sexual period; the numerous mictic females carried resting-eggs with a smooth surface. When the maximum was over, a new form with long

thorns appeared (fig. 25). During all three years of observation, the thorns were remarkably thick and curved outward during the months of July and August (fig. 27—28). In the latter part of September and in October the thorns were again parallel, and not so thick. During the beginning of May 1924 forms with short thorns similar to those from 4/VII 1922 reappeared, and during this period the mictic females carrying male eggs and later on resting-eggs were common. No sexual period was observed during 1923 when only long-thorned specimens were found. Already on 31/V long-thorned forms appeared again. It had no pronounced maximum in 1924, and all the forms were long-thorned.

Funke Pond. *A. aculeata* is most probably perennial, but usually it only occurs in small number; a maximum has occasionally been observed, in the spring (e. g. 1925) and never large; no sexual period has been observed. Always the typical form was observed, with long posterior thorns; these had a tendency to curve outward in the summer and simultaneously to grow thicker (fig. 15—18).

Schæffergaard Pond. *A. aculeata* only appeared sporadically during July—December 1906, but in March—May 1907 it was one of the main forms in the plancton; then in the last part of July 1907 it was again rather rare. A sexual period was observed in the first part of April; the mictic females carried 3—4 male eggs. On 6/V enormous numbers of females carried resting-eggs, and very many of these were lying free in the sample. The form is characterised by its size and very long posterior thorns (fig. 34—35), but in the winter and during the maximum in April (fig. 36—37) the size is much reduced and only forms like *brevispina* occur. Already on 23/V the large form occurs again; the few specimens from the summer all belong to this form (fig. 38); it is the *brevispina* form from March—April which carries the resting-eggs.

M. Pond. In one of my experimental ponds, where I had samples taken regularly from 13/III 08 to 18/X 08 *A. aculeata* was common on 13/III and had a well-marked maximum with a sexual period in April. The maximum lasted till ca. 15/V, then *A. aculeata* grew rare and only occurred in small number in the rest of the samples till 18/X.

During the maximum in March—April (fig. 6—7) it was only represented by a very small *brevispin* form; also forma *valga* occurred. But from the middle of May a somewhat larger form with well-developed posterior spines occurred (fig. 8); simultaneously the forma *brevispina* and *valga* disappeared, and the few specimens which were found from July to October were all very large with very long posterior thorns.

Summing up all our observations on *A. aculeata*, we arrive at the following results.

1. *A. aculeata* has been found in almost every pond, where investigations have been carried out; it generally seems to have a rather conspicuous minimum during the summer, but wherever it occurs it is common during the winter.

When samples are taken through holes in the ice, even if the ponds have been covered with ice for about 70—80 days *A. aculeata*, *A. cochlearis* and *Brachionus angularis* are among the principal forms of rotifers.

2. During the spring and occasionally during the autumn large maxima have been found, though never so large as those often observed in *A. cochlearis*; they have never caused a colouring of the water, as has been the case with *A. cochlearis*. Random samples taken in different ponds and at different times show that it is in the spring that mictic females appear. Apparently the females carry resting-eggs very long. Even if maxima at other times of the year are rather large, a sexual period has very rarely been observed; distinct proof of dicycly has never been given.

3. From my plancton investigation in 1901—1902 we know that *A. a.* is observed in all lakes in which observations have been carried out. There is always a maximum in May at a temperature of 8°—12° C.; on the other hand, a sexual period has never been observed in the pelagic region of larger lakes. This may be caused by a fault in the observations, but it may also be due to the fact that the species here really is acyclic or that new material from hatched resting-eggs is carried from the bays and littoral region into the pelagic region, and that a sexual period only occurs in the littoral stage of the life of the species.

4. As is the case with *A. cochlearis* the pelagic forms of *A. aculeata* from larger lakes do not vary so much as the pond forms; common to the *A. aculeata* of larger lakes are the hyaline lorica and the long, often well-developed posterior spines.

5. If the investigations are carried on in the ponds during the winter, it would seem, furthermore, that the variations in the species are in reality but slight. A form with well developed posterior spines is almost always common everywhere. If continued through the summer, the investigations will give quite another result, this is especially the case if only a single sample from a series of ponds is available. It may then be possible that the investigator will find as many forms as caused the older observers to create about 30 species, which were in reality all local and temporal variations of the same species.

6. If, furthermore, the investigator has at his disposal a series of samples taken the whole year round from a few ponds, it will be seen, as shown by LAUTERBORN with regard to *A. cochlearis*, that these temporal variations always begin in spring, reach their maximum in the summer, and disappear during the autumn, whereupon the main form predominates during the winter. It will further appear that some of these temporal variations occur in one pond, others in others. We invariably get the impression that these variations follow the great variations in external conditions, dependent upon variations in temperature and all other factors varying in accordance with it.

7. If however, as is now the case, we have at our disposal a series of samples taken from a fairly large number of localities, and as far as possible simultaneously, the picture obtained will in many respects be another.

As far as I can see, the seasonal variations are not only dependent on variations in external conditions, they also depend on an internal cycle, and are in some way connected with the sexuality and the development of mictic females.

8. My investigations seem to show that some of the most predominant forms such as *A. valga*, *A. brevispina*, *A. curvicornis* almost always appear before or during a sexual period. During this period the females have that peculiar appearance which makes us refer them to one of these seasonal forms; these seasonal forms may live for a shorter or longer period of the summer, but some time after the great spring maximum and the sexual period they disappear. During the summer the species is represented by specimens with well-developed posterior thorns of equal length, furthermore by forms which are on the whole larger than the spring forms. The number of them differs extremely from pond to pond; it is commonly small during the summer; greater during autumn, and may be rather large during the winter. In some ponds they are found in the summer in company with the forma *valga*, *brevispina*, *curvicornis*, in others alone; they may produce a large autumn maximum; during winter these forms (forma *typica*) with long thorns almost invariably occur.

From the fact that these long-thorned forms are the only ones derived directly from the resting-eggs deposited in the spring, we may suppose that they are hatched in different numbers at different seasons of the year. Many of the resting-eggs are deposited by the shore, and will then be left dry during summer; the raising of the water level will give them the necessary impulse; at very different seasons of the year often suddenly, and especially in a rainy autumn, great numbers of resting-eggs may be hatched. These large forms with well-developed posterior spines may perhaps have a sexual period and produce mictic females; as far as I can see, however, this is not the rule. Often, in Nature, the forma *typica* will be the main form the whole year round, and get a maximum during spring and autumn, owing to the hatching of enormous amounts of resting-eggs; often a decline in propagation will cause a slow decrease in number during the summer. In some ponds forma *typica* will predominate for two or three years, no sexual period will appear and none of the aberrant variations.

9. Sooner or later the irregular forms: *A. valga*, *A. brevispina*, *A. curvicornis* will then occur; and these forms are smaller than the main form, forma *typica*; they are less luxuriously developed. If both posterior thorns are developed they are small; in some ponds one of the posterior thorns is wanting, in others both; Simultaneously with the appearance of these forms the sexual period begins; the mictic females belong to all the above named forms.

10. The maxima, the sexual periods and irregular forms are followed by minima, large forms with well-developed posterior spines, and no sexual periods. During the minima the species may be present, but it is often so rare that it is difficult to find a single specimen. The few specimens may derive from resting-eggs hatched unusually early.

11. I am inclined to interpret these facts in the following way. Apparently sexuality sets in in the life of the colony when its strength is spent, and as if the sexual period is a process of renovation the main result of which is the resting-egg, from which the colony begins a new life with larger and more abundantly equipped specimens. The period of degeneration causing the sexual period seems not to occur in the history of the colony every year, often only every second year, or perhaps every third year. It often seems to be peculiar to a certain season, especially to spring-time; but this is not invariably the case.

It may occur in the autumn, but this has only been observed once, and may begin at the beginning of the winter. But if a colony is passing into a period of degeneration, the rule is that when the ice covers the ponds *A. aculeata* is present as forma *typica*, but with rather small specimens, while shortly after the ice has disappeared, at a temperature of 14°—16° C., the degenerative forms occur, whereupon a sexual period follows.

12. The variations in external conditions, especially with regard to temperature, viscosity and amount of nourishment, all influence the form of the organism, but in quite different ways; they affect the *curvature* and *thickness* of the posterior spines, very often these are curved very much outward during the summer; furthermore, the rough coating covering the whole surface of the carapace, and probably also the varying development of the facets of the carapace, are due to their influence. That they may likewise influence the size and varying degree of development of the spines cannot be denied, but in my opinion these factors are also dependent on the length of the parthenogenetic period.

13. In all our considerations one fact must not be lost sight of. As plancton organisms in larger lakes the species lacks all those forms which in my eyes must be regarded as degenerate. At the same time we know that in the pelagic region of larger lakes, as far as I know, no sexual period and no mictic females have ever been found. Apparently only amictic females occur here. We may find variations in size, locally as well as temporally, but the numerous pond forms have never been found as participants in the pelagic life of larger lakes.

This corroborates the fact that there is a connection between sexuality and the degenerate forms, but we have no clear explanation of why these forms do not appear in the pelagic region of larger lakes. It would be of interest if two branches of investigation could collaborate on this point so that experimental workers in the laboratory would select a colony which in Nature had been brought to the point when the irregular forms were just about to make their appearance, and by a thorough study either corroborate or weaken the views set forth here.

**Anuræa cochlearis** Gosse forma *typica* and **Anuræa cochlearis** forma *tecta*.

Plate VIII, fig. 1—21.

Frederiksborg Castle Lake. *A. cochlearis* is perennial. It has usually a considerable maximum in the latter part of May, after which it is commonly only

found in small number in the other samples. In 1924 it was by no means rare at the beginning of the winter, but then it seemed slowly to become rarer and rarer and when the ice had disappeared, it only occurred in small number; there was no spring maximum, and it was rather rare in all the samples the whole year round. In 1925 it had a great maximum in May, but then it became very rare again. A sexual period was never observed in the lake; mictic females carrying male eggs or resting-eggs were never seen. As they have been seen in other lakes, it is not very probable that they have been overlooked in this lake, from which we possess numerous samples.

The species had its normal very slightly varying aspect throughout all the years of observation; there was no pronounced difference in the length of the spine, and never transitional stages between it and *A. tecta*.

*Anuræa cochlearis forma tecta*. *A. tecta* occurs almost more sporadically than *A. cochlearis*. In 1923 the two forms apparently succeeded each other.

*A. cochlearis forma typica* had its maximum in the early spring, then *forma tecta* had a maximum in June and was common the whole of the summer, whereupon *A. cochlearis* only occurred in small number; only in the autumn the two species were almost equally common. In 1925 both forms were very rare in early spring, but on 25/V both forms had a very large maximum, after which they only occurred singly or were absent in the samples. Curiously enough, in this form, also, no sexual period was ever observed. A slow transition from *A. cochlearis* to *A. tecta* has never been observed. It seems as if the two forms are both well marked, and nothing seems to corroborate the view that one of the two forms is developed from the other.

Asminderød Pond. *Forma typica*. The occurrence is very peculiar. During the whole of 1922 it seemed almost always to be lacking in the pond. Then in December it appeared and was then one of the main forms during the whole of 1923 to the middle of June; then it disappeared again and was absent the rest of 1923. In 1924 it was only observed singly, and was totally wanting in several samples; a sexual period terminating the maximum in June 1923 was not observed.

*Anuræa cochlearis forma tecta*. It has been impossible for me to form any idea of the periodicity of *A. tecta*, especially with regard to its relation to *A. cochlearis forma typica*. Only one thing seems certain: it seems to disappear during the winter, or at all events to be extremely rare at that season. Whether the period when the water is covered with ice has been short or long, *forma tecta* always appears in May, whereupon it has its greatest maximum at the highest temperature; this maximum commonly ceases in the latter part of September, but it may, as in 1924, last till the beginning of November, in 1922 it even lasted to 22/XII, i. e. up to the very moment when the pond froze. In other words the maximum may occur at a temperature of about 24° C. and at 0° C. In this case too no sexual period nor seasonal variation was observed. Transitional stages between *forma*

*typica* and forma *tecta* have never been observed. Unquestionably forma *tecta* is the principal form in the pond. When forma *typica* had its large maximum in May—June 1922 *A. tecta* was absent; on the other hand, when *tecta* had its large maximum in the autumn of 1922 and from May 1923 and the rest of the year, *A. cochlearis* was almost wanting. They were only present simultaneously for a short time in June 1923. But also at that time no transitional stage between the two forms occurred.

Fredensborg Pond. In this pond hardly any form but *A. cochlearis forma tecta* occurs. In 1922 it had a very large maximum in the latter part of May and during the whole of June, then it disappeared and again had a large maximum in October—November, whereupon it became very rare. During the whole of 1923 it only occurred singly and only in rather few samples; forma *typica* was only found sporadically, but in several samples. A sexual period and transitional stages were never observed.

Island Pond. *A. cochlearis forma typica* is most probably perennial with a well marked maximum and minimum. Its occurrence is, however, not constant. This is only the case with the pronounced spring maximum which is largest in May. Then follows a summer minimum in July—August. This is usually followed by a rather low autumn maximum, which may last till the latter part of January, but commonly ceases in November—December. In August—September mictic females with three or four male eggs and with resting-eggs have been observed.

*A. cochlearis forma tecta* only occurs sporadically; in 1923 it was never found, in 1924 only in some spring samples, and in 1925 only in a single sample on 19/V. In the sample of 16/V 1924 mictic females with chains of 2—3 male eggs were observed. Transitional stages between the two forms have not been observed.

Nøddebo Pond. The main form is *A. cochlearis forma tecta*; forma *typica* was only observed in a few samples in October—December 1922. During 1922 *A. tecta* only occurred in a few samples; on the other hand, in 1923, it had an enormous maximum from the middle of April to the middle of July; so large that it coloured the water red. Then rather suddenly it almost disappeared, but was again common in August—September, and had a rather large maximum in October—November. Then it almost disappeared, but a fresh maximum developed in June 1924 and again in September—October. Mictic females with male eggs have occasionally been observed, but not in great numbers. Transitional stages which could lead to *A. cochlearis forma typica* have never been seen.

Horseshoe Pond. *A. cochlearis forma typica* occurs. It is perennial with a maximum in May—June and often with a smaller maximum in July—August. During the winter 1924—25 it was rather common.

Funke Pond. The main form is *A. cochlearis forma typica*. It is perennial and has a pronounced spring- or an early summer maximum, followed by a summer minimum, whereupon a new maximum sets in in the autumn. This may be enorm-

ous as in 1923, but is usually not so large as the spring maximum. In this pond a sexual period has often been observed in spring; mictic females with 2—3 male eggs are common, and numerous males have been seen. *Forma tecta* only plays a very unpretending rôle in the pond, always occurring singly and only in a few samples. Samples taken at different times during the years 1910—1924 show that *A. cochlearis* may occur in a form with an extremely short posterior thorn; simultaneously forms were found with very conspicuous facets on the carapace. All this was especially pronounced during June 1910. From May 1909 to April 1910 (fig. 1—2) the typical form prevailed; then in June, especially in the samples from 29/VI, all possible transitional stages between forma *typica* and forma *tecta* were present. It is very regrettable that we do not possess samples of a later date than June 1910, and when a sample was again at hand in June 1913 only *A. cochlearis* with a long posterior thorn occurred (fig. 3—12).

Almost the same phenomenon was, however, found in 1923 when *A. cochlearis* was again very short-thorned from June (fig. 13—21); the transitional stages however do not lead directly to a forma *tecta*; a very short posterior thorn remains. These stages are, however, very common after the great summer maximum. When this ceases, the species is rare, but it always appears in the above-named form. Conditions in Funke Pond show that the typical forms may predominate for several years; now and then it may be very similar to the forma *tecta* (1923), and in some years it may be reduced to this form. The sexual periods are always connected with the reduction period.

1. *A. cochlearis* has been found in Denmark in all kinds of water except dung water which it seems to avoid. It occurs in small ponds of some hundred square meters in size, the surface of which is either devoid of, or covered with vegetation. In ponds which had become desiccated in July—August, the species occurred as early as December (temperature 2° C.), when rain-water and melted snow had gathered in puddles at the bottom. It is common in the lakes in the downs of western Jutland; in the lakes of Raabjergmølle; in heath tarns and in puddles in the heath which are laid dry in June—July; it is one of the few species which occurs in our larger streams which do not serve as outlets for lakes. It is also common in brackish water (Ringkjøbingfjord, Stadilfjord, Limfjord); in other words, it is cosmopolitan in the widest sense of the word, more than any other rotifer.

2. It is a regular inhabitant of the pelagic region of our largest lakes. Most probably it is perennial there, but commonly it does not occur in great number. It has always a rather conspicuous spring maximum there, at a temperature of 13° C., then it is rare during the summer, but now and then attains a maximum in the autumn, which, however, is not so great as in the spring. During the winter it is always present everywhere as an inhabitant of the pelagic region, and also below the ice, but always in rather limited number.

3. It seems evident that in some years the species may almost be absent the



whole year round, and then suddenly, one year, develop huge maxima. This would seem to indicate that under certain conditions the species may rest a whole year or more as resting-egg, and that the huge maxima only develop under quite special conditions.

4. It further seems as if the period in which the mictic females appear is restricted mainly to the spring, though now and then they also appear in the autumn; on a few occasions mictic females have been found during the summer and at the beginning of the winter. In some ponds sexual periods have been found in the spring as well as in the autumn; this was also the case when the species occurred as a plancton organism in two lakes, Furesø and Sorøsø. In these localities *A. cochlearis* may therefore be regarded as dicyclic; on the other hand, I am by no means sure that the mictic females are always produced every year; I believe that there may be years in the life of a colony when it is acyclic. In this case as well as perhaps among most of the Rotifera it is therefore the amictic females which predominate perhaps for years, whereas the occurrence of the mictic ones is restricted to short periods.

5. As is generally known LAUTERBORN has pointed out a conspicuous seasonal variation, beginning in spring with *A. cochlearis typica* and finishing with *A. tecta* which is characterised by having no posterior spine. I must confess that I have only very rarely observed anything of the kind; I have only twice, in Funke Pond and in one of my experimental ponds, seen transitional stages between the two main forms *A. cochlearis forma typica* and *A. cochlearis forma tecta* and then only in a single sample and in a single year. In all the other ponds the two forms were always quite distinct; *A. cochlearis forma typica* is usually the main form, occasionally *A. tecta* predominates; if both forms are present in the same pond, one commonly predominates in one year and the other in the next. In a few cases both attain high maxima in the same pond and in the same year, but then the rule is that *cochlearis* predominates in spring and autumn, and *tecta* during the summer; only rarely do both occur simultaneously and with high maxima (Frederiksborg Castle Lake. Autumn 1923).

6. As transitional stages have twice been found it would seem beyond doubt that *tecta* is the last link in a developmental series beginning with *A. cochlearis forma typica*. On the other hand, the fact that in many ponds transitional stages have never been found, seems to show that the process by no means goes on in all localities every year and that the two forms at all events locally are formfixed.

7. Whereas with regard to *A. aculeata* it was possible to show that the periods when polymorphic tendencies are most predominant coincide with sexual periods, this has only rarely been the case with *A. cochlearis* (Funke Pond), most probably because the resting-eggs of *A. cochlearis* are not at a first glance distinguishable from those of the parthenogenetic generations.

8. Whereas, in contradistinction to the results of LAUTERBORN, *forma tecta* rather often was found at low temperatures, either in company with *forma typica* or alone, the

forms: *hispidata* and *irregularis* have only been observed during the summer; both may however occur together with the typical *A. cochlearis* as well as with the typical *A. cochlearis forma tecta*; *typica* as well as *tecta* may, during the summer, occur with a coating of short thorns giving them a brownish appearance; both forms may further show irregularity in the order of felts on the lorica. It is quite possible that, in these two varieties, we have seasonal variations, on the other hand I regard it as highly improbable that this is also the case with the abbreviation of the posterior spine. Here as with regard to *A. aculeata* I am much more inclined to think that internal factors, the distance from a sexual period, have exerted hitherto unknown influences.

9. The individuals of *A. cochlearis* which occur in lakes, are not apt to vary so much as those met with in ponds. The pelagic forms of *A. cochlearis* are on the whole rather distinct from those of the ponds; they are lighter in colour, more robust, commonly larger; they are never brownish yellow as those of the ponds, and have almost always a long, sometimes very long, posterior spine (*forma longispina*, Imh.). The different seasonal variations characteristic of the ponds have not been observed in the pelagic region of larger lakes, and when *forma tecta* is occasionally found here, it may be due to material which has been carried out into the lakes by means of affluxes and not to forms, the primary stages of which originate in the pelagic region of larger lakes.

#### **A. serrulata** Ehrbg.

This species is commonly regarded as one of the forms belonging to *A. aculeata*. This may be correct; on the other hand, it may be stated that in Denmark it is always found in localities of quite a special nature i. e. on *Sphagnum* and *Hypnum* moors, with extremely blackish brown water. It seems to live among the *Sphagnum*, from which it may be squeezed out when one squeezes a piece of the *Sphagnum*-carpet. It may also be found living in the small holes in these carpets, often in company with lyncodaphnid *Daphnias* and many species of Desmids. I have found it from early spring, the first days of March till late in November, a conspicuous sexual period with the mictic females carrying chains of four to five male eggs has often been observed.

This highly characteristic form, with its very conspicuous tessellate lorica with serrated ridges and the back of all spines jagged, with minute round pits, which cover every part of the surface, is restricted to peaty water. This circumstance and the fact that transitional stages between *A. aculeata* and it have never been found, makes it highly probable that we have here to do with a well-marked form now differentiated from *A. aculeata*.

#### **Anuræopsis hypelasma** (Gosse).

Asminderød Pond. *A. hypelasma* only plays a very subordinate rôle in the pond. It always occurs at the highest temperature of the water in July—

August, and disappears before October—November, and then it is also found in other ponds.

In Funke Pond it was a regular inhabitant of the vegetation in the free central part of the pond in 1900—1910. When the surface of the pond became more and more covered with leaves of *P. natans*, *A. hypelasma* slowly disappeared and from about 1920 it was only found in a few samples, and always sporadically.

*A. hypelasma* is a typical pond form and as such very common. It has only rarely been met with in the pelagic region of larger lakes. (Skanderborg Lake on 30/VII 1902 and Juel Lake 31/VI 1902). In contrast to the other *Anuræa* species it is a pronounced summer form, appearing everywhere in May and disappearing in the latter part of September. At temperatures below 12°—14° C. it only lives as a resting-egg. Whereas I have not found the mictic females in the above-named ponds, I have very often seen them during my summer excursions to many other ponds which I only visited occasionally. The mictic females carry two or three male eggs and one very large, brownish black resting-egg, still larger than the unusually large single summer egg which the female commonly holds pressed against the hollow smooth ventral plate of the carapace. The female is, however, also able to throw the egg backward, carrying it in a line with the longitudinal axis of the body, and in a slanting position. The mictic females always occur at the highest temperature of the water, most probably never for more than about a fortnight. Seasonal variation has never been observed.

### Notholca.

Of the *Notholca* species three species have often been met with. *N. striata* Ehrbg., *N. acuminata* Ehrbg., and *N. longispina* Kell; now and then also *foliacea* Ehrbg. has been observed.

It seems as if the *Notholca* species and especially those belonging to small ponds, covered in the summer with vegetation, have a peculiar predilection for low temperatures.

*N. striata*, *acuminata* and *foliacea* have all been observed in December, a little before the freezing of the ponds; their number is then but small, and this is also the case during the winter. Nevertheless, in years when the ponds thaw in the latter part of December or in January after a short freezing period it has been shown that these species now belong to the poor winter plancton of the ponds which is always present, and very often as main forms of the plancton. If a net is placed in the outflow from ice-covered ponds and smaller lakes, these *Notholca* species are always among the commonest rotifers. This means, in other words, that the resting-eggs may be hatched at temperatures very near zero, and that parthenogenetic propagation may go on at this very same temperature. Then when the ice disappears for the last time in spring, one of these *Notholca* species is often among the commonest Rotifera in these ponds; they belong to the central part of the ponds, but later on, when the surface is covered with vegetation, they entirely

disappear, and are only very rarely met with later on. In some ponds, or in the littoral region of larger lakes, or by the banks of the rivulets, now one now another of them may attain a fairly large or very large maximum, commonly followed by a sexual period; then when the mictic females have produced their male eggs and later on their resting-egg, the species disappears; a prolongation of the lifetime of generations of amictic females does not commonly occur. In the pond in the Botanical Gardens of Copenhagen, *N. acuminata* was extremely common during the whole winter of 1899 and had a very large maximum when the ice had thawed on 1/III; it had a sexual period on 15/III during which the mictic females carried chains of four to five male eggs and later on one or two dark resting-eggs.

On 28/IV 1913 another large maximum for *N. acuminata* was found in a small pond, Stutteri Pond, which dries up in the summer; mictic females were present, but already on 19/V not a single specimen could be observed.

On 25/V 1921 one of the bays in the little river Susaaen near my summer laboratory, contained an enormous maximum of *N. acuminata*; the specimens carried their eggs for a short time, but they were soon dropped off, and were then found at the bottom. Here also *N. a.* was in the middle of the sexual period; most of the mictic females were encircled in the vessels by numerous males; a week later not a single specimen could be found. *N. acuminata* and *striata* have also, during December—April, (temperature 2°—10° C.) been relatively often found in the pelagic region of our lakes; but the number of specimens observed was always small and mictic females were never observed.

#### ***Notholca longispina* Kell.**

During the exploration of the ponds in 1922 *N. longispina* was only rarely found, always sporadically and only in a few samples. About 1900 it was rather common in the first part of the summer in Frederiksborg Castle Lake, but later on it seems to have been much rarer.

At other periods it has often been found; its home seems to be rather large ponds with clear water; it has often been found in the little Vejlesø which is connected with Furesø; furthermore in Madum Lake in the north of Jutland, in Klare Lake at Hellebæk and in Løg Lake, both in the northern part of Seeland, only about 15 kilometers from Hillerød. The periodicity always seems to be the same. Where regular plancton investigations have been carried out, it seems to appear at very low temperatures; it may be present, but always in very small number, below the ice. The maximum sets in much later than in the other *Notholca* species, not before May—June, it does not occur before the temperature is 12°—14° C.

It may be enormous as was the case in Madum Lake on 20/V. The main part of the plancton consisted of *N. longispina*. As the sample was taken just at the time when the maximum was at an end, the water was filled with empty *Notholca longispina* lorica, which formed a regular vorridge at the bottom of the plancton net. Most of the females still alive were mictic, carrying resting-eggs.

Curiously enough, when I came back on 20/IX of the same year, the species was again extremely numerous and was again in a sexual period.

In Klare Lake, on 1/V 1923 at a temperature of the water of 10° C., *N. longispina* had an enormous maximum, and this was also the case on 23/V when, simultaneously, mictic females were found. In samples from June and September it only occurred in very small number.

In Løg Lake it had an enormous maximum in 1926 on 3/V and 19/V and in 1927 on 30/III, 28/IV and 19/V; only amictic females were found; they all carried a single egg. But already on 7/VI 1926 the species was extremely rare. The sexual period must have appeared between the two last named periods. During the rest of the year *N. longispina* was always present, but always only in a very limited number and always as amictic females. It was a little more common on 26/XII and had a large maximum immediately after the ice had disappeared on 30/III 1927. It was still present on 19/V when the exploration came to an end, because we could get no boat any longer.

Apart from these larger ponds and smaller lakes *N. longispina* is also found in the pelagic region of our largest lakes. Here its maximum is never large; it always occurs in June and at the beginning of July, in one lake (Skanderborg Lake) somewhat later. In the lakes it may be perennial, but after September it occurs in very limited numbers; the occurrence of mictic females seems to be restricted to the last part of May and the beginning of June and to temperatures about 15°—18° C.

A maximum with a sexual period was only once observed in Madum Lake also in September. *N. longispina* affords an example of these species which are periodical in ponds and smaller lakes, having a large maximum in May—June, terminating in the occurrence of mictic females which throw their resting-egg, whereupon the species so to speak disappears from the water-layers. In lakes the species is perennial, the amictic females having a very slow propagation after a very inconspicuous maximum, which however seems large enough to keep the species in an active stage in the water-layers all the year round.

It may be possible that a more thorough investigation may show some seasonal variation with regard to the length of the thorns, especially of the long anterior and the long posterior thorn; but such an investigation has not been carried out. —

## Gastropodidæ.

### Gastropus.

Four species are referred to the genus *Gastropus*, viz. *G. clavulatus* (Ehrbg.), *G. hyptopus* (Ehrbg.), *G. minor* Rousselet and *G. stylifer* Imh. In my opinion the genus should be divided into two, one containing the two former, the other the two latter species. — *G. clavulatus* is everywhere a very rare species. Hitherto it has not been found in Denmark.

**G. hyptopus** (Ehrbg.).

Plate VIII, fig. 22—27.

*G. hyptopus* is a pronounced pond form; it is mainly common in ponds covered with vegetation, and lives among the leaves of *Potamogeton* etc. When the ponds have a central part free from vegetation, it may happen that, during its spring maximum, it favours the "pelagic region", there feeding on *Peridinium* together with *Ascomorpha*. In some few ponds without vegetation, as Asminderød Pond and Island Pond, it may be found but always in small number and in few samples. It has a well-marked maximum everywhere during the spring, often at rather low temperatures, (about 6—10° C.). The samples may then contain hundreds. In the middle of April the sexual period occurs, and males are seen fairly often; the females do not carry the eggs; in the females have been found oval eggs, unquestionably carried by an amictic female, as well as a circular egg with a thick, smooth shell, most probably a resting egg. It is not known where the eggs are laid. They have no oil globules, most probably they drop to the bottom.

In figures 22—26 I have tried to give the main points in the anatomy of the animal. The great stomach fills almost the whole interior. When the animal is well nourished, the stomach almost always contains 4 large oil globules often symmetrically arranged; there is a large mastax-gland faintly divided into two parts. The enormous vitellarium containing numerous nuclei is a peculiar feature. When the animal is kept on inanition the cell structure of the stomach is visible, furthermore the muscle system, which is very difficult to study. The excretory canals are only visible when the animal is seen ventrally; they are remarkably short and have 4 vibratile tags. The skin is remarkably folded; the folds are given in fig. 26.

**Gastropus minor** Rousselet.

Plate IX, fig. 4.

This little creature seems to be rare everywhere; now and then it has been found singly in samples taken in very small ponds covered with vegetation.

In a little ditch near my home to my great astonishment I found on 20/IV 24 an enormous maximum of *G. minor*. The ditch was only  $\frac{1}{3}$  m. broad not a  $\frac{1}{4}$  m. deep and quite covered with vegetation. *G. minor* was present in thousands. The ditch had been covered with ice on 10/IV; on 12/IV the temperature was only 2° C., and the landscape was covered with snow.

During the period 15/IV—20/IV we had always frost in the night, and every morning the ditch was covered with ice. During the bright sunshine the ice thawed, and at 2 o'cl. the temperature of the water would rise to 10° C. The maximum lasted from about 15/IV—20/IV; on 26/IV the species only occurred in very small number. The eggs are thrown off on the vegetation, and very many were laid in my vessels. During the maximum amictic as well as mictic females were present.

The amictic ones carried a single large egg in the uterus; the mictic ones often about three much smaller eggs. The species was only present in the locality for about 10 days, and being much occupied with my *Asplanchna* studies, during these days, I had the misfortune to lose the resting-eggs as well as the males. Samples taken at the same time the two following years gave no *G. minor* and later it has only been observed sporadically. The ditch contained water to July, and in May—June it abounded in rotifers, mainly *Notommatidæ*.

As far as I have been able to see the animal does not possess the peculiar tube which characterises the mastax of *Gastropus stylifer*; nor is the skin so thick as in this animal. Here also the stomach is an enormous sack; it is doubtful if there is an anus. Gastral glands may be present but were not observed; the same is the case with the excretory canals which most probably lie on the very small ventral side. The vitellarium is very large and furnished with some large nuclei, the number of which is most probably eight. The dorsal organs have an oblique position very far behind; the foot glands are well developed. The eggs are deposited on algæ; the resting-eggs are unknown. The brown colour is highly characteristic of the animal.

### ***Gastropus stylifer* Imh.**

Plate IX, fig. 1—3.

*G. stylifer* has been found in Frederiksborg Castle Lake, Island Pond, Funke Pond and in Experimental Pond. In the first-named lake it has only been observed some few times, in the others it was found regularly for a few years; in 1898 it occurred in a long series of ponds and in all the following years very often. It seems to be absent or rare in water with high *Cyanophyceæ maxima* and unquestionably favours peaty water. The size of the sheet of water is of secondary importance; it has been found in small bog-holes, only of a size of a few square meters, and in the pelagic region of all our lakes. What is needed is only a water-mass free from vegetation; whether this water-mass is large or small is of no special significance, furthermore it seems to prefer clear water. —

Where it occurs, it is a pronounced summer form, appearing in May and commonly disappearing again in October, occasionally a few individuals may be found later. During the winter it has never been seen. It attains its maximum in ponds a little before the highest temperature, commonly in the latter part of May, in lakes somewhat later. The maximum is never large, and after its termination the animal only occurs in small number; in the latter part of May I have taken samples in several of the ponds and smaller lakes with several hundred individuals. In these samples there has been a very remarkable difference with regard to the size of the animals, the smaller ones being not even half as long as the largest. Simultaneously the *Uroglæna*-colonies carried oblong eggs, grey with blue markings. These eggs were hatched and gave *G. stylifer*. This observation was already made by LAUTERBORN (1898 p. 180). In this case, too, the summer eggs are laid on

other plancton-organisms. In cultures from 23/IV 24 from Funke Pond almost all the *Uroglena* colonies were covered with these eggs. In June the peculiar males were found. In another locality they were also found on 1/VIII 21. I have not seen the resting egg. LAUTERBORN (1898 p. 186) maintains that it is pelagic, and covered with bristles. —

In figs. 1—2, Plate IX I have tried to show some of the peculiarities of the anatomical structure of the animal. The skin is remarkably thick, but quite hyaline; the wheel-organ is strongly protruded in the figure. The long posteriorly bent tube issuing from the mastax and reaching the opening of the mouth is a highly characteristic feature; this tube is unique in the Rotifera; neither its structure nor its use is understood. It was first observed by ROUSSELET (1893 p. 448). Most of the body cavity is filled by the enormous lobated stomach containing numerous oil globules; it is rather conspicuously set off from the longitudinal striped rectum. The vitellarium is large, globular, containing eight nuclei. The excretory canals are not seen.

The foot is almost rudimentary, withdrawn when swimming, annulated and with faintly developed foot glands. As is generally known, this rotifer has the brightest colours of all rotifers hitherto known. The stomach is green, the body fluid red, the ovary and eggs are blue. The animals prey upon flagellata which they suck out. An anus was not observed most probably the digestion is intracellular.

*G. minor* as well as *G. stylifer* are both highly characteristic by their laterally compressed form; they are regular discs with a very small dorsal and ventral side. It is very difficult to make the animals stand edgewise; most probably the canals are only then visible.

### Ploesomatidæ.

The peculiar family *Ploesomatidæ* contains only a single genus, *Ploesoma*, including four species, *P. triacanthum* Bergendal, *P. lenticulare* Herrick, *P. truncatum* Lev. and *P. hudsoni* Imh.

I have found the three species *P. triacanthum*, *lenticulare* and *Hudsoni*. Of these *P. triacanthum* and *lenticulare* are pronounced pond forms; the first is by no means rare; it has mainly been found during the spring; its home is small ponds filled with vegetation; it swims very slowly, now and then moving its long foot, using it as a helm. It commonly carries a single large egg in its interior. Where it occurs, it is always found in relatively small number. With regard to sexual periods I have no information.

I have only found *P. lenticulare* on a single occasion in July in the ponds at Raabjergmølle in the northern part of Jutland.

### *Ploesoma triacantha* (Bergendal).

Plate IX, fig. 5—9.

In 1929 it was found quite accidentally in a little heath pond in the western part of Slesvig.



Some of the specimens have been used for the drawings, Plate IX, fig. 5—8. They give the peculiar ridges in the carapace (fig. 5—6), the enormous mastax, the small gastral glands and very large stomach overfilled with oil globules, the ovary with its eight nuclei and part of the excretory canals with two vibratile tags (fig. 5). Very conspicuous are the two palpar organs, one of which often is carried stretched backwards between the spines. It is a very slow-swimming animal. The colour is mainly brown.

### **P. Hudsoni** Imh.

Plate X, fig. 1—5.

In contrast to the other *Ploesoma*-species *P. Hudsoni* seems to be a pronounced pelagic organism, mainly occurring in the pelagic region of larger ponds, but also in real lakes. In the pond series mainly used for this investigation, it has only been found in a few summer samples in Island Pond.

It is a typical summer rotifer everywhere, never appearing before the latter part of May and disappearing again in October. As a plancton organism in lakes it has been met with in all the lakes which have been investigated. It is very ravenous, and preys mostly upon *Ceratium hirundinella*; when swimming it bores a hole in the shell of its prey and sucks it out. The summer egg is pronouncedly pelagic, surrounded by a thick gelatinous substance, in the centre of which the egg lies; the form and size of these eggs vary extremely. During the summer the egg is hardly ever lacking in the samples and well worth noting, because the pelagic region of fresh water, in contradistinction to that of the sea, contains so very few pelagic eggs, especially those which use jelly as a means to keep the eggs floating. It was already observed by ZACHARIAS (1893 p. 35). The resting eggs are not known with certainty. As I have, however, very often in all our lakes found in the autumn a rotifer egg agglutinated with a high thick foot of yellowish jelly to *Melosira* threads just at the time when *Ploesoma* is disappearing, I am fairly sure that we have here the resting-egg of *Ploesoma* (see also W.-L. 1904 p. 139). LUCKS (1912 p. 162) has found and drawn the eggs of the other species. I have tried in vain to keep *Ploesoma Hudsoni* in cultures. It invariably dies. It is an extremely vigorous swimmer, darting about, using its long foot as a helm; it does not rotate but swims in straight courses, often pursuing a single organism, especially *Ceratium hirundinella*. It never carries the eggs, the summer eggs may be dropped in the water, but in my vessels eggs were not found after isolated animals. — Curiously enough, though I have had numerous summer eggs under observation, none of them have been near the hatching stage, and I have never been able to keep them until the animal was hatched.

In two ponds in North Seeland, Løgsø and Sortesø, *Ploesoma Hudsoni* appeared with rather large maxima. This was in July; in September—October the animal disappeared. It was of course my intention to study this interesting animal and clear up the sexual period, the egg production etc. But at the very time when the sexual periods would most probably begin in the two ponds, it was impossible

for me to get a boat in either locality, and every attempt to get material from the shore was fruitless. Hence all my observations with regard to the salient point in the biology of the animal were quite insufficient.

On Plate X, fig. 1—4, I have tried to give the main structure of this highly interesting animal. The peculiar foam-like structure of the skin has been well figured by WIERZEJSKI and ZACHARIAS (1893). Situated dorsally in the skin (fig. 2) there is a very small shield, posteriorly carrying the dorsal organ; ventrally there are (figs. 2—3) two other shields in the angles of which the lateral organs are placed. The wheel-organ has two well-marked auricles especially conspicuous from the ventral side. The mastax is very large, containing the prehensile mouth-parts which are stretched out through the mouth-opening, when there is an opportunity of seizing the prey; it has two well-developed mastax glands with nuclei. The oesophagus is extremely large, folded laterally, a large sack extended dorsally, and ending in the rather small stomach with its large but relatively few cells and provided with the very large gastral glands, varying in form from specimen to specimen. I have once seen a defecation so I must suppose that an anus exists, but I have not with certainty seen the rectum. Hence it is not drawn in fig. 3. The excretory canals have a peculiar sharp bend in the middle of the body; the canals carry at least five vibratile tags. The contractile vesicle is large, lying remarkably far away from the hind-part of the body. The large ovary contains eight nuclei. The eggs when laid, are very small but in a few moments swell to their normal size. Their form (figs. 4—5) differs very much (globular, oblong). The annulated foot is extremely long, a powerful organ which, when moved from right to left, is able to alter the direction. It is one of the few rotifers which is able to swim in a vertical line without rotations when pursuing its prey; the foot glands are but slightly developed. The brain is characteristic by the long processes which it sends out into the palpar organs. The colour is a hyaline milky white.

#### **Asplanchnadæ.**

With regard to my conception of the genera and species of the family I refer the reader to the first part of my Contributions p. 254—256. The family comprises three genera *Harringia* (= *Dinops*), *Asplanchnopus* and *Asplanchna*. *Harringia* has not with certainty been found in this country.

#### **Asplanchnopus myrmeleo** Ehrbg.

Plate XI, fig. 1. Plate XIII, fig. 1.

*Asplanchnopus* has only been found in one locality, a remarkable stone-covered heath in the middle of Seeland near Sorø (Rejnstrup Oredrev). Originally it was only found in a single very small bog hole, filled with *Conferva* and with very peaty, almost black water. Later on it was also found in several small drying pools scattered over the heath. The number was always very small. Being far from my laboratory in Hillerød, it was impossible for me to get regular observations with regard to the propagation of this rare and very interesting species.

It was never found in spring; but on excursions in the latter part of July and in August several specimens were commonly observed; they were all amictic females, but once in October very large females with a yellow resting egg was observed. Cultures in the laboratory were attempted, but the animals invariably died in the course of a few days.

In July 1928 some males were observed. As the male has only been very cursorily described by WESTERN, WEBER and PLATE (W-L. Contributions I, p. 254) I have given a lateral (Plate XI, fig. 1) and dorsal view of it (Plate XIII, fig. 1). To the figures I only wish to add the following remarks. There is a rudiment of a mastax, but it contains no mouth parts; where it opens on to the forepart in the female there is, in the male, a peculiar groove covered with cilia; the alimentary canal is reduced to a peculiar bandlike body hanging down through the greater part of the body cavity and held in place by different muscles; at the sides there are two globular bodies, most probably the oesophageal glands; their form and size differ from specimen to specimen. In some of them they seem to be totally wanting; of a stomach there is not the slightest trace. The contractile vesicle is very large and furnished with two muscle cells. The testis has two prostata glands. The figures will presumably show the rest. —

### Asplanchna.

The species of the genus *Asplanchna* are very difficult to distinguish from each other. I shall here not enter into detail, but only set forth the following remarks. In my opinion the genus *Asplanchna* may be divided into two groups, those with a globular ovarium and those with a horseshoe-shaped one. The species belonging to these two groups differ very much from each other. *A. priodonta* especially is distinguishable from all other species owing to its form, the mouth parts, and the number of vibratile tags; the rare *A. Herricki*, hitherto not found in our country is noteworthy owing to a peculiar glandular organ near the opening of the urogenital organ. The organ has been regarded as a rudiment of the caudal glands.

It is the species of the group with a horseshoe-shaped vitellarium which cause the greatest difficulties. During more than 25 years I have had a very large material of *Asplanchna* forms with a horseshoe-shaped ovarium. At different times I have studied *A. ebbesbornii*, *A. Sieboldi*, *A. intermedia*, *A. amphora* and *A. Brightwelli*. The more I have seen, the more I have become convinced that it is impossible to retain more than two species of these and other forms, viz *A. Sieboldi* and *A. Brightwelli*. These two forms may most probably be distinguishable from each other owing to a very remarkable character: the nuclei of the vitellarium. In *A. Sieboldi* these are divided into three or four parts, whereas they are undivided in *A. Brightwelli*. The character was observed already by LEYDIG (1854), later on by HUDSON (1889 p. 121, Pl. XI, fig. 3 h) and LANGE (1911 p. 435). Hitherto I have only met with *A. Brightwelli* in rather large ponds, rarely in small very eutrophic

ponds which seem to be the home of *A. Sieboldi*. Often it totally disappears after a sexual period, but now and then it may be found the whole year round. *A. Brightwelli* may be found at all seasons of the year. The amictic females continue the slow propagation of the sexual period, while the mictic females disappear. In some localities it totally disappears after a sexual period.

As far as my experience goes, *A. Brightwelli* never forms winglike processes upon the sides of the body; on the other hand *A. Sieboldi* shows the highly remarkable fact that some of its colonies form one or two pairs of lateral humps or wings whereas in others these humps are not usually developed. Furthermore, the colonies which have commonly no humps are in some years, and under unknown conditions, able to produce humps; *A. Sieboldi* is a form which may have a uniform, dimorphous or even a trimorphous development; in most localities it has as a rule only one of these modes of development, but in some years it may suddenly show another. —

Neither in the structure of the forceps, nor in the shell structure of the resting-egg, or in the number of vibratile tags am I able to find valid characters. —

#### ***Asplanchna Brightwelli* Gosse.**

Plate XII, fig. 2, 3, 6. Plate XIII, fig. 2—4.

Frederiksborg Castle Lake. In this lake *A. Brightwelli* is a pronounced spring form, which arrives after the melting of the ice. The resting-egg may be hatched at a temperature near 4—6° C. The maximum differs greatly in the different years, but whether it is large or small, *A. Brightwelli* has always disappeared in the first days of June; the rest of the year it is totally absent, or at all events only present in very few individuals. During severe ice-winters it appears in small number below the ice. During 1925 it was only observed sporadically; during 1924, when it had a large maximum, it was fairly thoroughly studied.

Already from 29/III to 14/IV 1924 *A. Brightwelli* occurred sporadically below the ice. All specimens were amictic ones, whose propagation went on very slowly. By 29/IV the number was still very small and a maximum did not set in until 6/V. At that period a great number of large mictic female-producers were observed, each carrying one single large young one or a large embryo and about 10 eggs in different stages of development.

During the period 6/V—16/V the number increased enormously; enormous quantities were present especially at a depth of 2 m. Already by 10/V, only a week after the commencement of the large maximum, the mictic females appeared. Like the amictic ones they carried 8—10 eggs and young ones in different stages of development. Any pronounced difference in the size of the eggs in the two sorts of females could not be observed, and at the moment of birth males and females were almost of the same size. Isolated in small vessels the females lived at all events one week. On the same day (10/V) mictic females with resting-eggs were also observed. Many females carried two resting-eggs, both in the same stage of development, furthermore 5—7 eggs whose shell was not yet fully developed. If the plancton

is kept in large vessels, it may be observed that the mictic females with resting-eggs mostly avoid the light, whereas all the other individuals are to be found at the other side of the vessel, nearest the light.

The males are very numerous; in the body cavity of the females numerous spermatozoa are found, partly free-swimming partly in batches in different parts of the body-cavity. Females with two ripe resting-eggs and many unripe ones are found together with some possessing only two ripe eggs. In the former case copulation has taken place at a very early stage of the life of the mother animal, in the latter perhaps very late, the female acting as a male-producer before copulation. By 25/V almost all females were mictic ones, most of them with resting-eggs, many gave the impression of being old and spent ones. Very often I have had the opportunity of seeing females with one or two males swimming freely in the body cavity, the uterus having burst. These males swim round with the penis protuded and more than once I saw the penis of the male fastened to the ovary of the mother organism. Fecundation of the mother on the part of the son is by no means an impossibility. More than once I have seen the birth of the male. It always takes place in a moment; at the very moment of birth when the embryo passes the cloacal opening, a string furrow is observed which is pushed over the body; in a moment it, so to speak, divides the corpus in two balloon-shaped halves, then when the furrow has reached the end of the body, the male dashes out and swims away at the very moment of birth. The pairing process is often observed, always on the sides of the body, never in the cloaca, often near the wheel organ.

Already by 25/V the species decreased in number, and by 17/VI it was not possible to find a single individual. The whole development had not lasted more than about five weeks. It seems as if the amictic females, at all events in this locality, play only a very insignificant rôle in the life of the animal after the sexual period. In vessels with numerous *A. Brightwelli* the bottom is covered with resting-eggs; then the whole stock dies out. It is probable that in Nature too the resting-eggs sink to the bottom of the lake, but in early spring they may most probably rise from the bottom, presumably owing to development of air in the air-spaces of the shell. At all events, it is by no means a rare phenomenon in the first part of April, long before the development of the resting-eggs begins, to find resting-eggs floating freely in the plancton.

Asminderød Pond. The data of Asminderød Pond differ very much from those of Frederiksborg Castle Lake. In all three years of observation *A. B.* appeared in the latter part of May or in the beginning of June. The maximum which was always small, did not appear until July or the latter part of June; curiously enough, only amictic females were observed, but I presume that this was due to the small amount of material available for observation.

Fredensborg Pond. *A. Brightwelli* occurred almost only in 1922; it had then a rather large maximum in the latter part of May and during the whole of

June, when mictic females occurred; then the species totally disappeared, but already on 31/VIII it appeared again. By 6/IX several specimens were present, also mictic females with males, and free-swimming males; but already on 18/IX only one single specimen, a female producer, was observed.

Island Pond. *A. Brightwelli* had a rather large maximum in June 1898. During the investigation 1923—1925 not a single specimen was observed.

During the period 1898—1923 the species was often found during spring.

Horseshoe Pond. The species was absent in almost all samples. A few specimens were occasionally found, but on 29/V, 1924, there was a fairly large, very sharply delimited, maximum which seemed to terminate without any sexual period. Just at that time the huge Cyanophyceae maximum set in, and it may be possible that this in some way caused the termination of the maximum. —

Nøddebo Pond. *A. Brightwelli* was found neither in 1922 nor in 1923, but in 1924 a few specimens were observed in May—June and September—October. Mictic females were not observed.

Schæffergaard Pond. The species usually occurred in a few specimens in several samples and seemed to be totally absent from October to May. When the maximum of *A. priodonta* was over in May, a smaller maximum for *A. Brightwelli* (12/VI 07) set in, but later on it was extremely rare. —

1. During the last thirty years of observation *A. Brightwelli* has of course often been found accidentally during the numerous excursions carried out by me or my assistants. It has never been found in the pelagic region of larger lakes. Its home seems to be the central parts of rather large ponds e. g. Frederiksborg Castle Lake; it may be found in smaller ponds, even village ponds rich in organic matter, it seems however that the large maxima are only rarely developed here; I am inclined to suppose that a more thorough investigation will show that *Asplanchnas* with horseshoe-shaped ovaria and belonging to eutrophic ponds, when large maxima are developed, very often belong to *A. Sieboldi*. We have only rarely found it in peaty water.

2. In most localities a maximum occurs in spring, commonly a little later i. e. at a higher temperature than that of *A. priodonta*'s spring maximum. This maximum most probably always terminates in the appearance of mictic females which produce the resting-eggs, whereupon the species very often disappears. In contrast to what is the case with *A. priodonta*, it seems as if amictic females often are almost totally wanting after a sexual period. Now and then we have found a maximum with a sexual period in the latter part of September and in October, but this maximum has always been small. — During winter the species almost always seems to exist only as resting-eggs, and only in a very few cases have a few amictic females been observed below the ice. When this has melted, the resting-eggs may be hatched and a month later the maximum sets in. Specimens taken

below the ice in the Frederiksborg Castle Lake only very rarely carry young ones, at all events only a single one, and no eggs were ever observed; on the other hand, those taken in April—May almost always carried 1—2 large young ones and furthermore 8—10 embryos, in different stages of development. Furthermore, it must be remembered that amictic females hatched directly from resting-eggs in early spring are often exposed to temperatures only a little above zero, whereas those which derive from resting-eggs hatched in May or from later generations of amictic mothers are exposed to much higher temperatures. The mictic ones are not commonly exposed to temperatures much below 10° C., and often to temperatures about 20°.

As my material of *A. Brightwelli* taken at low temperatures was extremely limited, and as I was unable in my laboratory to follow closely the influence of temperature upon the rate of development of the amictic females, I only venture to conjecture that at the same temperature the amictic females live some days longer than the mictic ones; produce more young ones; and to a somewhat higher degree are able to accommodate duration of life and time of production of young ones to temperature. — TAUSON, too, (1925 p. 144) states with regard to *A. amphora* that the mictic females do not live as long as the amictic ones.

#### A. Sieboldi Leydig.

Plate IX, fig. 10—14. Plate XII, fig. 4.

In the limitation in which it is now taken, differing from that which I used in 1923 when I took *A. Sieboldi* and *S. amphora* Hudson as separate species, the species is most probably rather common in our country. Its home seems to be very shallow eutrophic village-ponds rich in organic matter and often covered with waterbloom. The species has been regularly studied in 1) a little pond Torkeri Pond, some kilometers south of Hillerød; 2) in Bistrup Pond near Furesø; 3) in Fjenneslev Pond near Sorø; 4) it has furthermore been found in 1900 in a little pond at Harløse mentioned 1923 (p. 263); 5) and in a little pond in Nøddebo about 7 kilom. north of Hillerød. All these ponds are only a few hundred square meters large; they are all extremely eutrophic ponds; all have large maxima of phytoplankton during the summer; the depth is never more than 1/2 m. In dry summers they may be totally desiccated. They are all almost free from vegetation. —

#### A. Sieboldi in Torkeri Pond.

A few kilometers south of Hillerød lies a little pond, Torkeri Pond, and near it a very little pond only about 10 m. long and 8 m. broad. As a rule it dries up every year and has no water from July to December when snow fills the depression; at the lowest level the depth is most probably only 1/2 m.; this is only the case in early spring, most years it is only 1—2 dcm. in May. In very moist summers it may have water almost the whole year round. During the process of desiccation it is divided into two parts, a larger and a much smaller one. The bottom

of the pond is grass-covered, and the leaves of the Gramineae are spread over the surface, forming a regular carpet upon it. From May the water is filled with Conferves, especially *Spirogyra*, which covers the inside of the net, when drawn through the water, with a thick green coating. — During the years 1900—1920 the little pond was often visited and its animal-life, especially that of *Hydrachnidæ*, *Diaptomidæ* and some *Trichoptera* subjected to regular observations. Now and then, especially in April—May, *A. Sieboldi* was observed, but hitherto only in small number. In the early spring of 1926, owing to investigations relating to other rotifers, I intended to visit the pond regularly every week. During the first days of April, shortly after the ice had disappeared, a few *A. Sieboldi* were found. It was more numerous in the succeeding samples, and supposing that the pond would dry up entirely in July, I concluded that the active life of the species could only be rather short. Then I subjected it to a more thorough investigation, which I combined later on with studies in the laboratory. During March 1926 the pond occasionally thawed, but owing to night frosts it was very often again covered with ice, sometimes for several days running. In an early spring sample later on (5/IV) *A. Sieboldi* was not present. On 14/IV the species was rare; all specimens were amictic. The pond was now visited almost every fifth day. Already on 19/IV the species was much more common, but still only amictic females were present. As early as 21/IV mictic females were present, some of them carrying resting-eggs. On 26/IV the desiccation of the pond was far advanced, and from now onwards the pond slowly divided into two ponds, a smaller and a larger one. In the smaller one with a water-level of only 1 dcm. the maximum was now enormous; very many mictic females with resting-eggs and males were present; in the larger one the maximum was also large, but here the females were mainly amictic; only few carried resting-eggs, and males were rare. On 1/V no great differences were observed. By 6/V, however, the maximum in the large pond was enormous; the greater part were mictic females, carrying resting-eggs; males were abundant. In the smaller part of the pond the development was already almost at an end; most of the females were without eggs; there were no males but, curiously enough, some amictic females.

Already by 12/V it was almost impossible to procure any more specimens; during the period 12/V—25/V a very few amictic females were present, but in the samples from 30/V and later they had totally disappeared. The water level was the same as about 12/V; during the summer of 1926 the pond never dried up entirely; samples were taken during the whole period June—November but *A. Sieboldi* was never found. During the period 14/IV to 12/V the temperature of the air slowly rose from  $+2^{\circ}$  to  $+14^{\circ}$ . The temperature of the water followed the temperature of the air; but on sunny days during the hours 12—4, the temperature of the water would sometimes rise to  $18-20^{\circ}$  C. Even though the pond was divided into two parts, there was water enough in both parts, but the vegetation was most abundant in the smaller pond. In both ponds there was, up to 1/V, an enormous



maximum of *Anuræa aculeata*; but from 1/V, and especially from 6/V, an enormous *Volvox* maximum was developed in the larger one; in the smaller pond it was rather inconspicuous. Till 1/V *A. Sieboldi* fed almost exclusively upon *A. aculeata* in both ponds, but during the period 1/V to 6/V the stomachs of *A. S.* in the larger pond were overfilled with *Volvox*; the animals were so to speak yellowish green; in the small pond the nourishment was almost exclusively *Anuræa* during the whole period.

As the main result of this little investigation it may then be established that:

1. The whole development of the species does not last more than a month, from the middle of April to — perhaps a little later than — the middle of May; desiccation of the pond sets no limits to active life after this time; for until July at all events the depth of the water is the same as when the species disappears in the middle of May.

2. The resting-eggs are hatched about 1/IV, and about 15/V new resting-eggs are formed and deposited, whereupon the colony dies out; its life in the active stage has only lasted one month; the other eleven months of the year are passed in the resting-egg stage, buried in the mud, trampled by the hoofs of the cattle which continually pass through the pond during the summer.

3. During the first week of its life the colony only consists of amictic females which produce large maxima owing to high fecundity.

4. Already in the second week the mictic females appear; during the last fortnight of the life of the colony it consists almost entirely of mictic females; a short time after these have died out some amictic females are present, then these females too die, and only the resting-eggs are left.

5. Whether the nourishment is pronounced animal food (*A. aculeata*) or it is rather suddenly altered to vegetable food (*Volvox*), the mictic females appear almost at the same time.

The life of *A. Sieboldi* is very similar to that of *A. intermedia*; this has been elucidated by the investigations of TAUSON (1925 p. 145). It was rare by 7/V and disappeared on 6/VII. Rapid development of amictic females in May; sexual period in the beginning of June; numerous mictic females on 22/VI; already on 26/VI they had almost disappeared. In my colony mictic females seem to have been much commoner than in that of TAUSON. In this case too *Anuræa* is the chief natural food.

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Simultaneously with the investigations in Nature large samples were taken into the laboratory. Here the material from all the days of observation was poured into large vessels and kept there during the whole period. At different times single females were isolated in small egg cups. The water was always that of the pond, and the food always either *Anuræa aculeata* or *Volvox*; into the small egg cups, the food was poured every morning by means of a pipette.

The material from large samples showed almost exactly the same development as that found in the pond.

Specimens were then taken from cultures dating from 14/IV, 25/IV and 3/V; from the first 5 specimens, from the other two, ten; a female was isolated, and as soon as it had thrown off a young one, this was isolated and kept with all its offspring. It was then seen that the cultures deriving from 14/IV consisted of amictic females only; they lived from 10 to 17 days, whereupon the colonies died out; mictic females did not appear. On the other hand, the 10 individuals isolated from the cultures of 3/V were all mictic females which immediately produced males; pairing took place; on the third day resting-eggs were present; in the course of 12 days all 10 colonies had died out, the females as well as the males; the resting-eggs were deposited on the bottom of the cup. In the ten colonies taken on 25/IV some consisted of amictic females, some of mictic ones; but those colonies which began with amictic females, consisted on the third day of a mixture of amictic and mictic females. They lived for 12 days; then the amictic females died, and the mictic ones had all deposited their resting-eggs.

These results are in accordance with what has been observed in Nature. The period begins with the production of amictic females and ends with mictic ones. During the middle of the period both kinds are found; at that time the maximum is increased by an enormous production of amictic females. After this the latter are gradually supplanted by the mictic ones, which are almost alone during the last part of the period. The peculiar thing is that the colonies dating from 14/IV died out in the amictic stage, and that males never appeared here. The colonies lived till the latter part of April, long after the period when mictic females had appeared in the pond. In my opinion it is quite incomprehensible why the colonies did not pass into the mictic stages.

In order to ascertain how long the amictic and mictic females lived, how many young ones they produced, and their distribution on the different days, the following experiments were carried out. —

10 females were isolated; as soon as a young one was born, it was observed; in the course of one or two days it could be decided if it was mictic or amictic. I got 5 mictic females born on 18/IV, and all of different mothers. These five mictic females were isolated, each in its cup and fed on *A. aculeata*. The cultures were watched till the death of the colonies; as soon as the males were born, they were removed.

Duration of life	18/IV	19/IV	20/IV	21/IV	22/IV	23/IV	24/IV	25/IV	26/IV	27/IV	28/IV	29/IV	Number of males
8 days No. 12 a	—	2	3	5	2	3	barren	death	—	—	—	—	15
5 — — 12 b	—	4	3	1	death	-	—	—	—	—	—	—	8
12 — — 2 a	—	-	2	5	5	2	1	—	—	—	—	death	15
8 — — 12 c	—	4	1	7	3	2	barren	death	—	—	—	—	17
12 — — 3 a	—	-	2	4	5	2	2	—	—	—	—	death	15

The following results may presumably be deduced from the table:

1. Supposing that the number (8) of males born (No. 12 b) is too low, I assume that the number of males normally born by a mictic female may be between 14 and 16.
2. The production of males begins already on the second, at latest on the third day.
3. The male production only lasts 5 days.
4. The females live barren 2—3, rarely 5, days after male production has ceased.
5. The greatest number of males is commonly produced on the third day.
6. In a single day a female (12 c) may produce 7 males.
7. The lifetime of the mictic female may be 10—12 days.

#### Culture No. 18.

- 20/IV. A mictic female, born on this day, is isolated immediately after birth.  
 21/IV. A male is born and 15 minutes later pairs with the mother animal.  
 22/IV. Conditions unaltered.  
 23/IV. Conditions unaltered. The male died.  
 24/IV. The female carries a resting-egg.  
 26/IV. The female now carries two resting-eggs.  
 27/IV. One resting-egg is deposited.  
 28/IV. The female again carries two resting-eggs.  
 29/IV. Conditions unaltered.  
 30/IV. The female died, but before death one resting-egg had been deposited.

#### Culture No. 19.

- 20/IV. A female isolated with one resting-egg.  
 21/IV. Besides the resting-egg, the female now contains two males.  
 23/IV. The resting-egg is deposited on the bottom; two males are born; the mother animal seems to be feeble, but still goes with one male.  
 24/IV. The female has now produced 4 males; the resting-egg is lying on the bottom; the female moves very slowly, the oviduct is distended in the shape of a sack, owing to the newly produced males.  
 25/IV. The female carries one resting-egg.  
 26/IV. The female now carries two resting-eggs; the males are all dead.  
 27/IV. The two resting-eggs are deposited.  
 28/IV. The female dies.

#### Culture No. 3.

- 17/IV. A mictic female isolated, age unknown.  
 18/IV. The female has produced 4 males.  
 19/IV. The female has produced another 4 males; 8 in all.

- 20/IV. The female dies.  
 21/IV. All eight males are still alive.  
 22/IV. The four males dead; the four living; a young female is added to the colony.  
 23/IV. The young female is alive; the four males died.  
 24/IV. The female carries a resting-egg.  
 25/IV. Conditions unaltered.  
 26/IV. do.  
 27/IV. do.  
 28/IV. do.  
 29/IV. The female died; the resting-egg not deposited.

#### Culture No. 20.

- 22/IV. A dead female is found with a living male in the uterus.  
 23/IV. The male is still alive swimming round in the body cavity of the female.  
 24/IV. The female is now only an empty skin with a decomposed wheel-organ; the male has escaped from the anterior part of the sack.

From these four cultures we are now able to deduce the following facts.

8. A mother animal may pair with its own first born son; according to TAUSON, ZAWADOWSKY (1916) has made the same observation with regard to *Diglena volvocicola* and LUNTZ (1926) for *Melicerta ringens* (p. 35) but not for *Pterodina elliptica* (p. 9).
9. The pairing process lasts about 2 minutes; it always takes place through the skin; pairing through the cloaca has never been observed. As soon as a male appears in a vessel in which there is a female, the penis is protuded; before the pairing the male continually encircles the females with the penis appressed to the skin of the female. When it has made a hole in the skin, the two animals can be taken up with a pipette and while still in connection can be brought under the microscope. Males seem to be ready to pair almost at the moment of birth; at all events a few minutes later; the pairing hole in the skin is visible during the whole lifetime of the female.
10. If the results deriving from culture 18 are compared with those from No. 19 it seems highly probable that pairing may be effective during the greater part of the life of the female.
11. If pairing takes place before egg-production begins, all eggs may be resting-eggs (Culture 18).
12. Culture 19 shows that a female may simultaneously contain resting-eggs and males. This is in accordance with the results of TAUSON (1925 p. 143) with regard to *Asplanchna amphora*.
13. Culture 19 furthermore shows that a female which has begun the production of resting-eggs may produce unfertilized eggs giving rise to males, and then

again produce resting-eggs, most probably after a second pairing process. This is in accordance with the results of TAUSON (1925 p. 143) for *Asplanchna amphora*, LAUTERBORN (1898 p. 179) and with those of ZAWADOWSKY (1916) for *Diglena volvocicola*, but not with those of MAUPAS (1890 a p. 312) with regard to *Hydatina senta* or of LEHMENSICK (1926 p. 51) with regard to *Euchlanis triquetra*; SHULL (1910) shows that *Hydatina* in a culture first lays resting eggs and then 23 male eggs.

The results deriving from cultures 18 and 19 are perhaps best elucidated by means of the following two tables.

## No. 18.

20/IV	21/IV	22/IV	23/IV	24/IV	25/IV	26/IV	27/IV	28/IV	29/IV	30/IV
born	pairing	—	—	1 R. egg	1 R. egg.	2 R.	deposited	1 2 R.	2 R.	death

## No. 19.

20/IV	21/IV	22/IV	23/IV	24/IV	25/IV	26/IV	27/IV	28/IV
1 R. ♀ with	1 R. and 2 ♂	1 R. dep.	4 ♂ born	1 R.	2 R.	2 R. dep.	♀ dies	
		2 ♂ born						

14. It is difficult to state the normal number of resting-eggs, but most probably it lies between 4 and 6; this is in accordance with the results of LEHMENSICK with regard to *Euchlanis triquetra* (1926 p. 50) and with those of SACHSE (1912 p. 52). The supposition of STORCH (1924 p. 329) and MARINELLI (1925 p. 163) that the Rotifera should only throw one single resting-eggs is unquestionably incorrect.

## Culture No. 11.

- 16/IV. An amictic newly born female is isolated.  
 17/IV. Conditions unaltered.  
 18/IV. The female contains a large egg.  
 19/IV. — — has now many large eggs.  
 20/IV. Conditions unaltered.  
 21/IV. Three young ones are born.  
 22/IV. Three other young ones born.  
 23/IV. Four other young ones born.  
 24/IV. The mother animal dies; there are 10 young ones, all amictic.  
 24/IV—6/V. The 10 young ones have been kept together in a large cup, are copiously fed and produce altogether about eighty young ones; all these young ones are amictic, all producing amictic females; during the last days one after the other dies.  
 by 6/V. The whole colony has died out. —

## Culture No. 21.

- 14/IV. 10 amictic females are isolated from the vessel.  
 14/IV—5/V. During the period 14/IV—5/V the 10 females produce very many (about 100) young ones, but all these young ones are amictic and by 5/V the whole colony dies out.

From the cultures No. 11 and 21 we are nowable to deduce the following facts.

15. The lifetime of the amictic females cannot be given with certainty; in my cultures they all died out too early. Their lifetime most probably depends in a very high degree upon the temperature. From my observations in Nature I have the impression that they may live much longer than the mictic ones, especially at low temperatures, and that the number of young ones which they produce, may be distributed over several weeks at low temperatures and at high temperatures be crowded into only a very few days.
16. Cultures 11 and 21 seem to corroborate the peculiar fact that, especially during the beginning of the whole developmental period, families may occur which consist exclusively of amictic females; at all events it has not been possible, when special experiments have not been carried out, to see them pass to the propagation of mictic females. This result is in fairly good accordance with that of the authors who maintain genotypic reaction (SHULL 1911); RUNYANZEW (1923 p. 37) maintains, with regard to *B. urceolaris*, that in all his 7 generations the males arrived at quite distinct periods, quite independently of all variations in external conditions.

## Culture No. 1.

- 17/IV. 10 amictic females isolated each in a cup by itself.  
 18/IV. The 10 amictic females have each thrown from 2 to 5 young ones.  
 19/IV. The 10 amictic females have now thrown each from 5 to 10 young ones.  
 20/IV. Some of these young ones have now young ones ready to hatch.  
 21/IV. In one of the cups a mictic female is born; this culture is now studied, it contains an old female, now barren, dating from 17/IV, furthermore 6 young ones, of which it may be shown that four are mictic, two amictic.  
 22/IV. The old female dies; the four mictic females have now produced 6 males, the two amictic ones, four amictic females.  
 23/IV. The four mictic females have now produced 12—14 males; one female with a resting-egg.  
 24/IV. Males are numerous; most of the females carry resting-eggs; the amictic females have either begun to produce mictic females or, if not, their young ones do so.  
 25/IV. Males are numerous; most of the females carry resting-eggs; some resting-eggs are deposited.  
 26/IV. The males die; conditions are otherwise unaltered.

- 27/IV. All males die; many resting-eggs deposited.  
 28/IV. Many females die, some with resting-eggs.  
 29/IV. All females dead; most of them have thrown their resting-eggs; a few have died without having done so.

## Culture No. 5.

- 16/IV. A female, presumably amictic, is isolated.  
 17/IV. At 11<sup>1</sup>/<sub>2</sub> o'cl. a young one is born; at 2 o'cl. two others.  
 18/IV. Conditions unaltered: a mother with three children.  
 19/IV. Now five young ones. —  
 20/IV. The five are distended by many and large eggs, the old mother has borne two new young ones; all in all 7.  
 21/IV. There is now the old mother and 10 young ones; some of these will probably produce young ones in the night.  
 22/IV. Present are now 11 large females, 7 very young small females and 12 males; the progeny of the old mother was partly females which produce amictic females like itself, partly females which produce mictic females. Many pairings are observed.  
 23/IV. Conditions unaltered; many males, but no females with resting-eggs.  
 24/IV. Conditions unaltered; the old female from 16/IV dies.  
 25/IV. Conditions unaltered.  
 26/IV. The males die out, but one of the mictic females still produces males; most of the others carry resting-eggs.  
 27/IV. All males dead; almost all females carry resting-eggs; some are deposited.  
 28/IV. Conditions unaltered.  
 29/IV. Conditions unaltered; many resting-eggs deposited.  
 30/IV. Many females die; several with resting-eggs.  
 1/V. All females dead; many resting-eggs deposited, but several in the dead mothers.

## Culture No. 9.

- 17/IV. 40 females are placed in a little vessel; no males.  
 18/IV. Many females carry resting-eggs and there are many males.  
 19/IV. There are now about 100 males; some females carry three resting-eggs; some females are amictic, producing many or a few amictic young ones.  
 20/IV. Conditions unaltered.  
 21/IV. Conditions unaltered; many resting-eggs deposited.  
 22/IV. The males begin to die, almost all females carry resting-eggs.  
 23/IV. Conditions unaltered; all males dead.  
 24/IV. Conditions unaltered.  
 25/IV. Conditions unaltered only more and more resting-eggs are deposited.  
 26/IV. Conditions unaltered.  
 27/IV. Conditions unaltered.

- 28/IV. Conditions unaltered, but the females now begin to die.  
 29/IV. Many females dead; the bottom covered with resting-eggs.  
 30/IV. All females dead; bottom covered with resting-eggs.

From the cultures No. 1, 5 and 9 we are able to deduce the following facts.

17. Cultures 1, 5 and 9 should illustrate how a colony passes from amictic to mictic propagation.

No. 5 shows that an amictic female is able to produce females which produce amictic females like itself as well as females which produce mictic females; this is only what might be expected. TAUSON (1925 p. 144) comes to the same result; with regard to *A. amphora*. LEHMENSICK's supposition (1926 p. 51) that we have to do with three different kinds of females among the Rotifera is most probably incorrect.

External or internal conditions may force an amictic female to produce females which produce amictic females like itself as well as females which produce mictic females; but the last named females do not appear until some time after the colony has begun its life. Most probably at all events the female hatched from a resting-egg is always and solely amictic, as also the following generations. LUNTZ (1926 p. 30) has arrived at the same result with regard to *Pterodina elliptica*.

A combination of investigations carried out in Nature and in cultures seems to show that we have here really periods at the beginning and at the end of the lifetime of the colony when amictic and mictic propagation is fixed, and that these two extremes are interrupted by a labile period where a combination of influences of internal and external conditions may cause variations in the propagation giving rise now to amictic now to mictic colonies.

#### Culture No. 25.

18. To ascertain the lifetime of the males 10 males were isolated as soon as they were born; they got no opportunity to pair. The 10 males lived for the periods stated below

	1	2	3	4	5	6	7	8	9	10
Number of days . . .	4 <sup>1/2</sup>	3 <sup>1/2</sup>	4	5	4 <sup>1/2</sup>	4 <sup>1/2</sup>	3 <sup>1/2</sup>	4	5	3 <sup>1/2</sup>

For the unpaired the lifetime seems to be about 4 days; but if the males have an opportunity to pair, their lifetime is shortened by one or two days; a male may pair several times.

19. It may be pointed out that mictic females of *A. Brightwelli* and *Sieboldi* which have produced resting-eggs and whose lifetime is perhaps abnormally prolonged about 8 days in cultures, often carry about 8—10 eggs in their uterus, which are of different sizes, remarkably dark, and seem to be undeveloped resting-eggs. In (Tab. XII, Fig. 6) a female with these eggs has been shown.



20. Furthermore it may often happen that the last developed males are not born in a regular manner. A rupture of the uterus takes place, and a male may be found swimming round in the body cavity of the female. The female may live for 2 or 3 days. Then it dies and decomposes. The male still lives and at last the body wall of the female burst and the male is set free. Tab. XIII, fig. 3—4 shows this. —
21. It is a feature peculiar to the form from Torkeri Pond that it never shows humps of any kind. During its whole period of active life it looks like a typical *A. Brightwelli* but an examination of the vitellarium shows that the nuclei are all divided into three or four parts and this has been the case during the whole development. —

*A. Sieboldi* in Bistrup Pond.

In the above named pond in Bistrup near the borders of the Furesø I found an *Asplanchna* in the latter part of June 1929 which had the normal form and structure of an *A. Brightwelli*. Nevertheless I had the impression that perhaps it belonged to those peculiar forms which could later on be changed into humped forms; a closer examination showed that the nuclei of the vitellarium were divided into three or four smaller parts. A regular investigation was therefore carried out.

It was only present in a very few specimens on 25/VI, and still rare by 11/VII. Then rather suddenly, on 22/VII, it was one of the main forms of the plancton; it was still common on 2/VIII—12/VIII—22/VIII—28/VIII but on 9/IX was only present in a very few specimens; later on it totally disappeared. Its periodicity may be given as follows:

25/VI	11/VII	22/VII	2/VIII	12/VIII	22/VIII	28/VIII	9/IX	20/IX	3/X	24/X
w	v	cc	c	c	c	c	w	0	0	0

On 25/VI and 11/VII only the normal form appeared; however from 22/VII to 28/VIII all forms were humped (Tab. IX, fig. 10—12); on 9/IX again only the typical forms appeared. Tab. IX, fig. 10—12 shows sketches of the form; the transition from the saccate to the humped form took place quite suddenly in the course of only a week, this is in accordance with the observations of LANGE (1911 p. 438) who maintains that the humped forms appear suddenly in the third generation.

On 11/VII only amictic females occurred, but on 22/VII very many carried resting-eggs (Tab. IX, fig. 14) and males were common. These males are all humped (Tab. IX, fig. 13). On 2/VIII most of the females had laid resting-eggs but males were still present; the same was the case on 12/VIII when mictic and amictic females were found in the samples, but the number of the last-named seems to have increased. On 22/VIII and 28/VIII only amictic females were present, and with the presence of a very few amictic females on 9/IX the development stops.

The whole active period of life lasted from the last days of June to the first days of September, only a little more than two months; the presence of mictic females and males was restricted to the period from 22/VII to about 15/VIII i. e. to about three weeks. At the beginning of the sexual period the humped females appeared, and these were the only forms during July—August. The males were almost absent from 22/VIII; they were of the typical humped form.

Upon studying the anatomy it was impossible for me to find any differences from the typical *A. Sieboldi* form in spring; the ovary is horseshoe-shaped with numerous divided nuclei, an ovary of a young animal is drawn in Tab. XII, fig. 2. The number of vibratile tags is 20—30, a little lower than is commonly stated for *A. Sieboldi*. The mouth-parts are of the typical *Brightwelli-Sieboldi* type and so are the resting-eggs. As is well known from earlier investigations (POWERS, LANGE), we have here a colony which may as well be referred to the typical *Sieboldi* as to the form which has been termed *intermedia* and which is most probably identical with *A. amphora*.

In Bistrup Pond it therefore seems that we have a *Sieboldi* form which regularly, at the highest temperature of the water, produces humped forms, and whose males always seem to be humped. In the last part of the period of active life the specimens reverted to the saccate form; most of the humped forms are mictic females, but amictic females may also be found among them.

#### *A. Sieboldi* in Harløse Pond.

As mentioned in 1923 (Vol. I, p. 262) *A. Sieboldi* was found here only once in July 1898 in a very small eutrophic pond near Harløse a few kilom. west of Hillerød. The pond was only a few metres in diameter. When visited later on the pond had altered very much and most probably became totally desiccated. The species has never been found again. The animals were in the middle of the sexual period. Very many males and mictic females with resting-eggs were present. A few females belonged to the saccate form but most of them were pronounced humped forms, and so were all the males. The animals were large, ca. 1800  $\mu$ , and extremely hyaline; the humps longer and more pronounced than in those of Bistrup Pond; the cells of the vitellarium were conspicuously divided into three or four parts. —

As the form has totally disappeared after 1898 I have been unable to follow its life cycle.

Most probably it will have been similar to that in Bistrup Pond, and so also the seasonal variation will have been the same, perhaps only a little more pronounced.

#### *A. Sieboldi* in Fjenneslev Pond.

With regard to the pond see under *B. pala*. When found on 10/VIII 21 the species was in its sexual period. Males and females with resting-eggs were present in great number. All observed females were pronounced humped forms and so

were the males; they were very much like the specimens from Harløse Pond. The pond was very often visited during the years 1922—29. In 1924 and 1929 the pond froze to the bottom. Curiously enough, after 1921 only very few *Asplanchna* specimens were found. Many samples were taken during May—August. Most years only a few samples contained *Asplanchna*, and these always belonged to the saccate form. Then suddenly in 1925 the *Asplanchnas* were again numerous, and again the humped forms appeared. I am indebted to my assistant, Mr. Berg, for the samples taken in 1925.

3/V	15/V	3/VI	9/VI	15/VI	7/VII	15/VII	25/VIII	31/VIII	7/IX	4/X	31/XI
0	0	0	0	0	0	w	ccc	cc	cc	0	0

It will be seen that the species appeared on 15/VII but only in a few specimens. 25/VIII it had an enormous maximum which lasted till 7/IX. In September it disappeared again. After 1925 only a very few specimens, always of the saccate form, appeared. As such they also appeared on 15/VII but during the period 25/VIII to 7/IX only humped forms with humped males and females appeared.

We learn from this that the development of humped forms does not necessarily take place every year. We do not know what life conditions cause the humped forms to appear but it seems that they only appear in these years when the great maxima occur.

#### *A. Sieboldi* in Nøddebo Pond.

As mentioned in 1923, p. 264, *A. Sieboldi* was found in Nøddebo Pond in the latter part of August 1921. I regret to say that I have nothing to add to what has been written there. As mentioned there, the species showed the same very peculiar trimorphic development which POWERS has described (1912, p. 441). The colony was followed during the rest of 1921, and with the greatest interest I looked forward to the moment, the next year, when I was to begin laboratory work with this very interesting species. The pond was regularly visited every fortnight during 1922 and, as will be seen from the table V, all through 1922—1924. In the following years, too, samples were taken every fortnight and often in connection with studies on the *Daphnia pulex-longispina* races carried out by my assistant, Mr. Berg. Every week during the summer months in the years 1925—1929 samples were likewise taken. Year after year the character of the pond altered more and more, it was filled with confervas, in 1929 with *Elodea*. It is now very shallow having only a depth of a few decim; and has now no more a central part free from vegetation.

It is very difficult to interpret the facts in the right way. Two months before the *Asplanchna* was found (August 1921) the pond was laid dry and the bottom dug up. When the pond was again filled with water, the depth was about  $\frac{3}{4}$  m. The water was a peaty brown; there was not the slightest trace of vegetation; *Daphnia* and Flagellates had great maxima. In that year *Asplanchna* with a full trimorphic development was very common. I refer the reader to part I, 1923.

The colony was followed till 15/XI when *Asplanchna* had disappeared. Only a few saccate forms were present; the humped form predominated; the later observed specimens were of the campanulate form. Resting-eggs appeared in the campanulate and humped forms. It is a peculiar fact that after 1921 only very few *Asplanchna* were observed in the samples during the period 1922—1925; after that time no *Asplanchna* have been observed. The pond is now stocked with confervas and *Elodea*; the vegetation is so thick that the surface of the pond looks like a meadow.

Being unaware of the character peculiar to *A. Sieboldi* — the division of the nuclei of the vitellarium into three or four parts — I described the species as *A. amphora* in 1923, as this was the only species in which a trimorphic development had been observed. The specimens observed during the period 1922—1925 were all according to their form *A. Brightwelli*.

I am inclined to suppose that the *Asplanchna* from Nøddebo Pond 1921 may be referred to *A. Sieboldi*. In 1921 it was the first time after the investigations of POWERS (1912) that a trimorphic *Asplanchna* was observed, and as far as I know, it is the first time it has been found in Europe. It would be of the greatest interest to see if an *Asplanchna* with a trimorphic development would appear again when the pond is once again laid dry, the bottom dug up and the pond again gets a surface free from all vegetation. At a given moment the bottom must have contained innumerable resting-eggs which either have not been developed or whose young ones are killed immediately after hatching.

POWERS has pointed out that all the three forms, the small saccate females, the humped ones, and the campanulate ones carried resting-eggs, and all were able to produce males. I for my part have only been able to find resting-eggs in my locality, and males in the two last-named forms, the saccate form being rare and disappearing totally already in the latter part of August. We do not know if both forms of females the amictic and the mictic ones, are able to undergo the same trimorphic development, or if trimorphism is limited only to one of them. This makes it more difficult to understand the whole development. From POWERS' investigations we know that the females hatched from resting-eggs are always of the saccate form, furthermore they are always amictic. Then follows a series of amictic saccate forms whereupon partly mictic ones, partly humped and campanulate forms appear. The relation between the mictic forms and the trimorphism of the species is not explained, and I regret that I have had no opportunity to continue the valuable investigations of POWERS and MITCHELL.

*A. Sieboldi* as it is treated here is an extremely interesting rotifer. It belongs to small eutrophic, most probably alkaline, ponds. In numerous localities it looks like an *A. Brightwelli* only distinguishable from it by the peculiar structure of the nuclei of the vitellarium. In some localities it has a tendency to dimorphism, to develop humped forms from a saccate form at the period when the mictic forms appear. It seems as if this dimorphism is not developed every year in the same

locality. The appearance of the humped forms is quite sudden, the colony passing from one form to the other in a single generation and in a single week. The saccate form produces the humped forms, and later on in the autumn, the humped form the saccate one. Most probably the amictic as well as the mictic females produce both forms.

It is to be supposed that under quite special conditions the species may be trimorphic, producing saccate as well as humped and campanulate forms. This trimorphism has only been observed twice, once by POWERS and MITCHELL at Lincoln, Nebraska, and one year in a little pond in the northern part of Seeland.

### *Asplanchna priodonta* Gosse.

Plate XII, fig. 1, 5. Plate XIV, fig. 1—2. Plate XV.

Frederiksborg Castle Lake *A. priodonta* Gosse has in almost all the years of observation had a larger or smaller maximum in the latter part of May and in the beginning of June. Beyond this period the species seems to be extremely rare. This holds good especially for the three last years of observation. Most probably the species has a very large maximum in the above-named period, but like *A. Brightwelli*, as soon as the resting-eggs appear, the species seeks deeper waterlayers or perhaps sinks deeper owing to the greater weight of the resting-eggs, and in this way it more easily evades observation. The number of specimens which appear after the melting of the ice is always small, and they are not able to produce the often enormous and rather sudden maximum which appeared e. g. on 11/VI 24. It seems as if huge masses of resting-eggs are hatched during April and the first part of May. The amictic females, present in the middle of May, always contain a very large number of young ones and eggs in different developmental stages, often 8—12, the largest of the young ones have already before birth almost fully developed young ones; i. e. three generations develop within each other, the third generation being born the day after the mother animal itself is born. That these amictic females play a great part in the sudden appearance of the high maximum is unquestionable. Before the latter part of May the samples teem with males; the mictic females have appeared, and almost simultaneously females carrying resting-eggs are present. I have never seen a female carry more than one resting-egg; as is generally known, the egg-shell has no airspaces, on the other hand the egg always contains oil globules.

In the latter part of May or the middle of June the species disappears almost at a sweep from the water-layers. Males and mictic females disappear almost simultaneously, amictic ones being extremely rare during the rest of the year. Only in one year (1900) there was a tendency to develop a maximum in September—October, but mictic females were not observed. The few amictic females occurring from June to April next year always carry only one young one, differing very much from those from May which carry a great number.

Island Pond. In all three years of observation (1923—25) *A. priodonta* had a large spring maximum, always occurring in the latter part of May; it could be present in small number throughout July and then disappear almost totally from the plancton. Only in 1923 rather a large maximum appeared again in the last days of August. During spring mictic females with resting-eggs and males have always been observed. In 1900 as well in many others years during the period 1900 to 1923, we have seen large spring maxima and hardly ever found *A. priodonta* after July. Immediately after the melting of the ice no specimens are observed; they do not appear until two or three weeks later, and these females are always amictic. Here as everywhere else the amictic females are enormously prolific in May, but at all other seasons of the year the few observed females only carry a single young one. —

Horseshoe Pond. *A. priodonta* occurred with larger or smaller maxima in May—June in all the three years of observation, but apart from that time was rare. In May 1923 it had a pronounced sexual period; and curiously enough another, but smaller one, occurred in October—November, but the maximum was then relatively small; nevertheless it was dicyclic in 1923.

Funke Pond. *A. priodonta* is most probably perennial; larger maxima have not been observed, or if so always in May—June. — During the years before 1922, especially during the period 1898 to 1910, the spring maxima were much larger; later on, simultaneously with the restriction of the "pelagic region" of the pond, owing to the increase of the *Potamogeton* zone which slowly conquered more and more of the free central part of the pond, *Asplanchna* became rarer and rarer each year.

In one of the previous years I had had an opportunity of observing how huge a rotifer maximum may be. Lying in my boat one of the last days in May 1910 with bright sunshine on the pond, I saw at a depth of only 1 m. (maximum depth of the pond about 1½ m.) a milky layer stretched out over the whole bottom. In the surface layer there was the usual life, which will be found noted in the table of the pond. Dipping the net into the milky layer, it could be seen that it consisted exclusively of *A. priodonta*. It was in the beginning of the sexual period. —

Schæffergaard Pond. *A. priodonta* is almost absent from July to November but it begins to be more common in November and has, curiously enough, a pronounced sexual period in November. Another occurs in April—May, whereupon the species disappears in the beginning of July.

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During the last thirty years *A. priodonta* has been found most probably on every excursion where a plancton net has been used, and where several ponds have been visited.

It is impossible to prove any predilection for special ponds or special compositions of water. *A. priodonta* requires a free water-mass, devoid of vegetation,

but this water-mass need only be some few cubic meters in a bog hole, on the other hand it may also be one of our largest lakes: It is present in peaty water, and in water with high *Cyanophyceae maxima* rich in organic matter. —

It generally seems to have a pronounced spring maximum in ponds; in May—June the mictic females appear, whereupon lots of resting-eggs are found. Amictic females often seem to play a rather conspicuous rôle during the rest of the year, and it is possible that the autumn maximum, when the temperature has again sunk to that of spring, originates from an increased propagation of these females. —

Wherever a more thorough investigation has been carried out, it has been shown that in May the amictic females are filled with brood in different stages of development, whereas at all other seasons of the year they only carry one or two young ones. The amictic females are very often found in small number below the ice, but just these specimens seem to have almost suspended all propagation under natural conditions. In 1898 I have, in a few ponds where *A. priodonta* was common, found mictic females as well as males in the winter at temperatures near zero. When studying the same ponds in 1924—28 I saw nothing of *Asplanchna*; the ponds had altered in different ways during the last 25 years, and many of them were covered or filled with vegetation.

As a plancton organism it has been found in all the larger lakes observed in 1898—1902. There it is everywhere perennial, commonly the maxima do not seem to be great, and where they occur, they always develop in spring; in 1901 mictic females were observed from 18/V to 22/VI. Only in Esrom Lake an enormous maximum with a sexual period was observed on 5/IX 01 (temperature 16). — In lakes, too, the species are always found during winter at temperatures near zero and here, too, always as amictic females whose production of eggs has almost entirely stopped. —

As the resting-eggs contained large oil globules, I supposed that they must be pelagic. They have never been found in the pelagic region. I have kept mictic females in vessels  $\frac{3}{4}$  m. high. The resting-eggs were invariably dropped into the water and sank to the bottom. Further investigations should aim of finding out if they are to be found floating in the deeper water-layers especially in early spring.

As mentioned above, I was unable to get sufficient material for my studies relating to the propagation of *A. Brightwelli* at low temperatures. This, however, was not the case with regard to *A. priodonta*. I could get *A. priodonta* in early spring from Frederiksborg Castle Lake as well as from Løgsø, a little lake about twenty kilom. southward from Hillerød. The difficulty was to get sufficient natural nourishment; especially during the first period the nourishment was most probably small, but I suppose that this was also the case in Nature. It consisted of other rotifers, taken from Frederiksborg Castle Lake, where they were caught every day and by means of a pipette sucked up into the light border of the vessel.

On 15/III, 23 cultures were started, each culture containing a single *A. priodonta*, caught the same day in Frederiksborg Castle Lake; with regard to the temperature

of the lake it may be mentioned that the winter was extremely mild; until 15/II the lake had only been frozen about 12 days, and rarely over the whole surface. From 15/II to 25/II the lake was frozen, but at the inlet of the lake there was always open water and here samples were taken. From the middle of December to about 1/III the temperature of the lake was always about zero; from 1/III to 10/IV the temperature of the water was from  $+2$  to  $+5^{\circ}\text{C}$ ., rather heavy snow and night frosts prevented a rise in temperature.

Not until 28/IV was a temperature of  $+8^{\circ}\text{C}$ . observed. — In nature the *Asplanchna* have lived from December to the latter part of April at temperatures between  $0-5^{\circ}\text{C}$ . In the laboratory the cultures were standing in a room where the temperature of the air did not exceed  $+6^{\circ}\text{C}$ ; but this temperature was rather constant, varying only from  $5$  to  $7^{\circ}\text{C}$ . —

Of the above-named cultures many died, but some of them lived from 15/III to 8/IV i. e. for 30 days; in the following the main results from these cultures are given.

As soon as a young one was born, it was taken away. Only in culture 14 were the young ones kept with the mother animal.

Culture No. 9 c.

The young one born 15/III, lived 22 days without having produced a single young one.

Culture No. 9 d.

The young one born 15/III, lived 18 days and in these eighteen days produced two young ones.

Culture No. 13.

The young one born 15/III, lived 21 days, in that time producing three young ones.

Culture No. 16.

A female which has lived at all events for 22 days has produced 5 young ones.

Culture No. 14.

A female produces six young ones in the course of six days, itself and its young ones produce 14 young ones in 17 days.

The following cultures originate from *Asplanchna priodonta* taken 28/III in Løgsø, and are continued to 18/IV.

Culture No. 15.

A female whose age is unknown produces 4 young ones in 18 days. When fresh water is given, they all die. —

Culture No. 29.

A female whose age is unknown, produces 6 young ones in 22 days and then dies.



All these cultures are not so satisfactory, as might have been desired. I wished to give the animals the natural food, especially other rotifers and mainly *Anuræa*. At that time of the year it was not possible to get material enough to feed the animals regularly. The often rather sudden birth of several young ones in a few days and then none for a long period, may be put down to the irregular supply of food. On the other hand, the cultures clearly show that these *Asplanchna* born at temperatures near zero and living at a temperature of 5—6° C., live much longer than those at temperatures 14—16, and that their propagation goes on very slowly. I am inclined to think that the *Asplanchna* living at temperatures near zero and below the ice, may live very long, perhaps for months, and that they have almost suspended all procreation for weeks. That there is the greatest difference between these winter *Asplanchnas* and those of late spring is beyond doubt, if we compare them with those which I have studied during the high maximum in May in a small pond lake as Frederiksborg Castle Lake.

The investigations give no information with regard to the conditions under which the resting-eggs may be hatched.

From observations of the periodicity it may be concluded that especially those of *A. Brightwelli* may hibernate. The results gathered from the literature differ very much. According to TAUSON (1925 p. 145) the eggs of *A. intermedia* freeze for five months. LEHMENSICK (1926 p. 53) gets resting-eggs of *Euchlanis triquetra* hatched in the summer after 1½—2 months, PLATE (1886 a) those of *Hydatina* in the course of 18—21 days; SHULL (1910 p. 311) gets eggs hatched in the course of a few days to many weeks.

### The sack-like *Asplanchna priodonta* Forms.

Tab. XV.

In 1898 (p. 207), I showed that two female forms of *Asplanchna priodonta* occurred in the small Farumsø, one of the ordinary round type, the other sack-like, elongated-oval, the longitudinal and transverse axes being as 5:1. In August all conceivable transitional stages between these two forms occurred. For a long time round embryos were observed in the females of the round type, and only oval embryos in those of the elongated type, but round embryos were met with in the latter on 25/VIII.

I had no idea whatever of seasonal variation at the beginning of my investigations, when I discovered these very peculiar and at that time unknown conditions. I considered them as peculiar phenomena of growth, and imagined them to be derived from distinct and separate broods.

In the following years similar phenomena were discovered in Furesø, where the sack-like forms, however, were exceedingly rare, furthermore in Haldsø, in Thorssø near Silkeborg, and in a lake in the south of Funen. In the other Danish lakes, on the other hand, only the ordinary small round or slightly oval *A. priodonta* forms were met with. Further investigations showed that the oblong forms first appeared

everywhere in May—June and reached their greatest length in July—August whereupon they disappeared.

These particular forms made me study the seasonal variations more thoroughly and led to my later paper (1900 p. 606). Later on VOIGT (1904 p. 109) discovered quite similar conditions in the lakes of Ploen. During the cold months the typical forms occurred, but in summer elongated sack-like animals.

VOIGT is, as far as I know, the only one who has seen these peculiar forms. HUBER (1905 p. 128) has studied the seasonal variation in the Montiggler Lakes, but in contrast to VOIGT and myself arrives at the conclusion that the individuals are smaller in summer, not more than about 470, whereas in the colder season they may reach 730.

Finding that the *Asplanchna* in Haldsø and Farumsø were excellently adapted for a more detailed study of the way in which seasonal variation occurs, I had collections made regularly in Haldsø and Farumsø during the period May—September 1902. Unfortunately, the species proved to be so rare in Farumsø in 1902 that the necessary material could not be procured; in 1905 the long sack-like females were not observed at all. From Haldsø, on the other hand, I obtained excellent material which has been used for the following studies. There are samples from 3/V—30/V—11/VI—17/VI—22/VI—25/VI—3/VII—9/VII—18/VII—1/VIII.

In each of these samples 50 individuals have, as far as the material permitted, been separated off, and their length and breadth measured; if the animals contained a comparatively large embryo, the latter was also measured. The ratio between length (L.) and breadth (B.) has been calculated, and the percentage of animals of the same length.

Six months after I had finished my investigation of the *Asplanchnae* the work of LANGHANS (1906 p. 439) was published. Since the relation of *A. helvetica* to *A. priodonta* is fully explained there, and I entirely agree with LANGHANS on this point, I need only make reference here to his work. IMHOF's species *helvetica* may be looked upon as a local variation of forma *typica*. I should think that it may best be termed a cold-water form belonging to the larger cold lakes; whether it is correct to consider it specially alpine remains undecided.

In my Plancton Investigations Vol. II these measurements have been given (p. 78—81). Referring the reader to this work, the main results of the investigations of 1908 are reprinted here.

The investigation clearly shows that the shape of *A. priodonta* in Haldsø has undergone very considerable changes during the period 3/V—9/VII. Tab. XV shows the seasonal variations.

The first remarkable fact is that the variations in shape take place within a surprisingly short period, from the end of May to the middle of July when the species disappears, i. e. a period of hardly more than a month and a half. *A. priodonta* which was mostly between 560 and 640  $\mu$  long and about 400 broad on 30/V was on mostly over 1600 9/VII, whereas the breadth was only about 480—560.

Consequently the species increased very considerably in size in the course of about 5 weeks, but the growth was almost exclusively in the longitudinal direction of the animal, the breadth remaining almost unchanged. Whilst the ratio  $\frac{L}{B}$  was about  $\frac{1.5}{1}$  at the end of May, never  $\frac{2}{1}$ , the same ratio was mostly  $\frac{3}{1}$ , in the beginning of July, and might even reach  $\frac{5}{1}$ . It should further be noted that the volume of these long sack-like summer forms is much greater than that of the small winter forms. With regard to the shape of the long summer forms the figures show that the longer the animals grow the more curved the body becomes. Though I have no clear understanding of this phenomenon, I believe that it may be interpreted as a means to augment the cross-section resistance. As far as I know, the long axis of the body has a sloping position when the animal is swimming; then the curved part of the body will augment the cross-section resistance during sinking. It may be remarked that on examining these very large sack-like *Asplanchnæ* in Haldsø in the living condition in July 1906, I found that, as for the living *Asplanchnæ* in Farumsø in 1898, the ratio  $\frac{L}{B}$  was about  $\frac{5}{1}$ . If we compare one of the forms from Haldsø with a normal *A. priodonta*, it will be seen that the prolongation mainly takes place in that part of the body which lies behind the urogenital opening, furthermore that all organs in the first-named species are not much larger than in a normal *A. priodonta*. The number of vibratile tags is only four, and the mouth-parts are exactly similar to those of *A. priodonta*.

The increase in the longitudinal axis may presumably take place in three ways:

1. The seasonal variation may be of a purely individual nature; in the animal, the ratio  $\frac{L}{B}$  of which is  $\frac{1.5}{1}$  on 30/V, the longitudinal axis keeps on increasing during the succeeding month without any particular increase occurring in the transverse axis. This explanation implies that the individuals occurring on the 9/VII are the same as those met with on the 30/V.

2. The seasonal variation may not be individual, but connected with the occurrence of new broods; in the same individual the ratio  $\frac{L}{B}$  remains unchanged; seasonal variation occurs through the longitudinal axis in the embryos being longer relative to the transverse axis than it is in the mother-animal. Thus the seasonal variation is not due to a gradual growth in one direction in the mother-animal, but proceeds intermittently in connection with the occurrence of new broods.

3. The seasonal variation may be due to both of these factors.

On measuring the embryos inside the mother-animal it appeared, firstly, that the longer the mother-animal is, the longer is the embryo. On the 30/V when the mother-animals were mostly 560—640, the largest embryos measured were 400—480. On the 9/VII when the majority were 1600, the largest embryos were 1000—1280.

This is not so very remarkable in itself; it is of far greater interest that over 60 measurements of the embryos inside the mother-animals all gave the result that the longitudinal axis of the embryos had increased at the sacrifice of the transverse axis in a higher degree than was the case with the mother-animal. The transverse axis of the embryos could always divide the longitudinal axis more times than the transverse axis of the mother-animal could divide its longitudinal axis, i. e. the embryos are always longer and narrower than the mother-animals.

Thus, whilst the ratio  $\frac{L}{B}$  in the mother-animals on the 30/V never reached  $\frac{2}{1}$ , the same ratio in the embryos was  $\frac{2.5}{1}$  or  $\frac{3}{1}$ . Similar results are met with on all other dates recorded. It further seems as if these differences between embryos and mother-animals are greater at the beginning of the period, at the end of May and the beginning of June, and smaller towards the end of the period; when the difference in the ratio  $\frac{L}{B}$  in the mother-animal has reached its maximum in the beginning of July, the difference in  $\frac{L}{B}$  in the embryo in comparison with  $\frac{L}{B}$  in the mother does not increase very much; yet it will be seen that, whilst there are very few mother-animals on the 3/VII in which  $\frac{L}{B}$  is much more than  $\frac{3}{1}$  and while it very rarely reaches  $\frac{4}{1}$ , the embryos are mostly  $\frac{4}{1}$  and may even be  $\frac{5}{1}$ . I may remark here, that the embryos are less exposed to the pressure of the cover-glass; the ratio  $\frac{L}{B}$  in mothers and embryos cannot, therefore, be compared directly without some reservation. Nevertheless, the difference is not of such a nature that it can in any way alter the main result. Thus it is shown with absolute certainty that the seasonal variation is connected with the occurrence of new broods. The transverse axis always divides into the longitudinal axis a greater number of times in the embryos than in the mother-animals; seasonal variation results from this. See Tab. XII, fig. 1 and the series on Tab. XV. In the animal of 9/VII three generations are found in each other.

It is much more difficult to show that seasonal variation is also of a purely individual nature; nevertheless, this may be the case, and for the following reason.

It appears from the statements above that the small size of 560—640, in which the  $\frac{L}{B}$  was always  $< \frac{2}{1}$ , constitutes 80 % of the *Asplanchna* on 30/V, but on 11/VI only 6 %. At this time a very abrupt rise in the sizes may be discerned, there being not less than about 90 % of 800 or more with  $\frac{L}{B} > \frac{2}{1}$ , while only 6 % are about 560—640, and all intermediate sizes are wanting. As late as 25/VI a few individuals of the size 560 and with  $\frac{L}{B} < \frac{2}{1}$  occur; consequently, the shape of the latter has remained unaltered.

After 11/VI, on the other hand, the increase of L. goes on quite gradually. The size 800—1200, represented on 11/VI by 90 % is still on 17/VI represented by 46 %, on 25/VI by 12 %; on 3/VII this size seems to disappear. A new one of 1200—1440, represented on 17/VI by 50 % has increased in number to 60 % on 20/VI and on the 25/VI to 82 % but has decreased to 16 % on 3/VII. A new size of 1520—1600 appears on 25/VI with 8 %, increasing on 3/VII to 56 % and probably still more on 9/VII. At the same time the ratio  $\frac{L}{B}$  increases gradually from  $< \frac{2}{1}$  to  $\frac{2}{1}$  and later on to  $\frac{3}{1}$  or even  $\frac{4}{1}$ .

I am inclined to interpret these facts to mean that the small females of about 560 with  $\frac{L}{B} < \frac{2}{1}$  represent forms which have been hatched from resting-eggs and carried into the pelagic region. The great majority of these die before the 11/VI, a few live longer, but this first generation does not undergo any seasonal variation whatever; in these females the ratio  $\frac{L}{B}$  is unchanged from the time of hatching to the time of death.

The matter is different for the following generation. — There is nothing to justify the belief that this generation, which appears mainly at the end of May, is unable to live till the latter part of June. As we now know that the largest, and most probably also the oldest, of the egg-bearing individuals are likewise those which have the greatest difference between L and B, and as this difference increases quite gradually and no more abrupt transitions occur in the sizes, I conclude that this generation undergoes seasonal variation. When first hatched, its length in proportion to its breadth is greater than that in the mother-animal (ca.  $\frac{2}{1}$  or more) but this disproportion increases further during growth and is still greater ( $\frac{3}{1}$  or generally  $\frac{4}{1}$ ) before death.

Further, a great number of generations probably arise during the period 11/VI—3/VII, all of them being alive at the same time; they are not hatched at the same time, but their death for the most part occurs about the same date: the middle of July. These generations, when hatched, are always longer than the mother-generation, and during their growth L constantly increases more than in the previous generation. B for the most part remains unchanged. — The result of this is that in the beginning of July we have young, very narrow animals which are exceedingly elongated, their  $\frac{L}{B}$ , while they are alive, being at least  $\frac{5}{1}$  or possibly more. From the middle of July or rather somewhat before, the majority of the individuals are sterile; the series of generations ends in these long sack-like animals, in which egg-production is very much reduced or which hardly ever produce eggs. I never saw resting-eggs in these females or any small round females which might have connected this generation with conditions in the spring. All observed females were

amictic. It is as if the species, through these long sack-like individuals with  $\frac{L}{B} = \frac{5}{1}$ , has gone beyond the limit of variation, and that these curious-looking individuals must pay for their existence with sterility.

How development proceeds after July, I am unable to say as regards Haldsø. *A. priodonta* disappeared from the water in August almost at once, in October—November a very few, small, round individuals occurred again with normal  $\frac{L}{B}$ . These individuals remain throughout the winter and spring, until the above-mentioned progression of generations begins again at the end of May. Neither males nor resting-eggs have ever been observed.

In Farumsø, on the other hand, the long sack-like females persist much longer; here I once observed small round females inside the long sack-like individuals at the end of August. In autumn males also occurred and the small round females carried resting-eggs; the males had a normal appearance; I have never seen the long sack-like females carrying resting-eggs.

Apart from these two lakes I have hitherto only found females with  $\frac{L}{B} = \frac{4}{1}$  in the Furesø and in the small Thorssø near Silkeborg. In the Furesø there were but a few individuals, probably conveyed thither from Farumsø, they occurred in Thorssø in immense quantities in the summer of 1901—1902, but only a few samples were taken.

In order to understand the occurrence of these peculiar sack-like plancton forms, the following must further be remembered. The home of the *Asplanchnae* is in the central parts of the low, overgrown ponds and small lakes, among the vegetation of which their near relation, *Asplanchnopus*, and most of the *Asplanchna* species live. Two of the species, *A. Brightwelli* and *A. priodonta*, have become adapted to the life in the free, central parts of the ponds and small lakes. Both are carried out into the pelagic region of the larger lakes by the outlets, but only one of them, *A. priodonta*, accommodates itself to the life there, so different from the conditions of life in the true home of the species. In the ponds *A. priodonta* does not undergo any noteworthy seasonal variation. Nothing of the kind has ever been observed abroad, and in my own country I have studied the matter in many different ponds every fortnight throughout a year without observing it;  $\frac{L}{B}$  is always  $< \frac{2}{1}$ .

It is mono- or dicyclic in ponds, with a distinct sexual period in spring and often one in autumn; the parthenogenetic reproduction in spring is very rapid, in spring it will often happen that 5—6 embryos are found in the same mother-animal and half-developed embryos are often seen in unhatched embryos.

In the lakes, *A. priodonta* probably always undergoes some seasonal variation;

but this has hitherto escaped notice or has been misinterpreted. — After becoming acquainted with the conditions in Haldsø, I directed my attention to the species in other lakes. Here I often observed  $\frac{L}{B}$  to be  $\frac{2}{1}$ , but never more. The very same result is obtained on comparing the drawings and measurements of other plancton investigators (APSTEIN, HUBER, VOIGT etc.) with the drawings and measurements given by those who have studied pond individuals, HUDSON & GOSSE etc. — This more elongated lake form is identical with *A. helvetica* IMHOF.

We see, therefore, that in the lake forms there is a tendency to increase the longitudinal axis which is not present in the pond forms, and in this I see an adaptation to the new claims made by the new surroundings. As it is now sufficiently proved that the ratio  $\frac{L}{B}$  in the winter forms of the lakes is identical with that in the pond forms, and that the increase in the longitudinal axis does not set in till the temperature of the water rises, and increases steadily with the latter and simultaneously with the general increase in the longitudinal axis of numerous plancton organisms, there is in my opinion no other explanation possible than that the seasonal variations in *A. p.* are adaptations to all those variations in external conditions which are connected with the changes in temperature.

The different degrees in the seasonal variations, viz. the varying increase in the ratio between the longitudinal and transverse axis, can on the whole be provisionally referred partly to race peculiarities and partly to the unequal influence exerted by the conditions tending to produce variations. Continued investigations in numerous lakes and ponds will probably show localities with all conceivable transitional stages between the small almost round, and the large sack-like, individuals; further I imagine that continued investigations over several successive years in the same locality will show that the ratio  $\frac{L}{B}$  is very variable in the different years.

If it should prove, as I suppose, that the elongated sack-like females in many lakes become in the end sterile, and that production of mictic females does not occur, I should be inclined to look upon these individuals, at any rate in many localities, as pond and littoral material carried out regularly every year into the pelagic region in the form of the small round individuals, which give rise to the elongated individuals and perish as such without leaving any young. The pelagic region is then recruited from the littoral region each spring when the embryos are hatched from the resting-eggs, which are produced exclusively by the individuals of the littoral region and are spread all over the lake by the waves.

If this is the case, the elongated, sack-like females may best be considered as pathological individuals which have come too near to the utmost limit of elasticity of the species. As I once found an almost isodiametric embryo inside one of the elongated sack-like females with  $\frac{L}{B} = \frac{5}{1}$  in Farumsø in the autumn, there is

also a possibility that these are constant and normal seasonal forms, and that they produce parthenogenetically the winter form which survives the winter and is met with again in Haldsø on 3/V and 30/V. As I have only met with one case and have never found even a single specimen of the kind in Haldsø, though the material was rich enough and my attention was directed to the point, the observation is in great need of corroboration. The absolute disappearance in August and the peculiar phenomenon that the series of generations ends in individuals which are almost exclusively sterile, in my opinion point to the truth of the former explanation, at any rate as regards Haldsø.

What highly favours the development of the lake races to which these forms belong is the fact that they only reproduce parthenogenetically; it seems as if they only consist of amictic females. External conditions may deal as they like with the species; there is no amphimixis that could prevent the formation of the seasonal forms, and once the direction of variation is determined, they being always under the same influences, tend always to reproduce in the same way, until they have reached their limits of variation.

It must further be emphasized that the *Asplanchnae* naturally need not always respond to the demands for diminishing the rate of sinking by changing their shape from spherical to cylindrical. The same demand may also be met by a relative increase in surface due to a decrease in volume. HUBER has observed this phenomenon in the *Asplanchnae* of the Montiggler Lakes; they are there smaller in summer than in winter, and the decrease seems to be equal for both axes.

### Melicertidæ.

My few observations on sessile, not free-swimming, species seem to show that most of these species are pronounced summer forms. This is the case with *Megalotrocha albo-flavicans* Ehrbg. found near Susaa, in Tjustrup Lake, *Lacinularia socialis* (Pall.), *Oecistes mucicola* Kell., common in *Gloiostrichia pisum*, *Oecistes pilula* Wills. on leaves of *Nuphar* in Funke Pond, Hillerød, *Oecistes melicerta* (Ehrbg.) found on *Nuphar* leaves in October in Funke Pond, Hillerød, *Limnias ceratophylli* Slack. in different ponds near Hillerød, and *Melicerta ringens* Schrank in numerous places in the northern and middle parts of Seeland, in Gudena, Jutland, etc.

### *Lacinularia socialis* (Pall.).

*Lacinularia socialis* was found in Jutland at Ry, Gudena. The coast-line of the rivulet was covered with trees, and from them a carpet of roots is hanging down into the water. On drawing them out of the water, it was seen that the roots were covered with innumerable balls, all of a peculiar reddish colour, and as large as peas. Observations from a boat further showed that the banks of the river over a stretch of many hundred meters were literally covered with a thick coating



of these ball-shaped colonies, which when more thoroughly studied were determined as colonies of *Lacinularia socialis*. The phenomenon was observed in July 1898 and unfortunately upon a journey; how long this almost incredible maximum of this beautiful species had lasted and when it again disappeared, I do not know. Later on I have twice visited the spot but without result; the colony-coatings had disappeared. In one of the experimental ponds, Carlsø near Hillerød, the *Lacinularia* colonies appear on the *Nuphar* and *Nymphæa* leaves in the latter part of June about two or three weeks after the leaves have reached the surface. The number of colonies increases in the course of the summer, many leaves carrying about fifty colonies or more. Till the first part of September the colonies have been quite amictic, but then numerous male eggs and males appear; mictic females are now present, and in the latter part of September numerous resting-eggs are deposited in the jelly. Already in the first part of September, when the lower side of the leaves begins to be coated with thick carpets of diatoms, detritus etc. the number of colonies diminishes, and bare spots show in the brown coatings, where the colonies have had their place.

#### **Melicerta ringens** Schrank.

In some of our ponds *Melicerta ringens* is extremely common on the floating leaves of *Nuphar* and *Nymphæa*. In one of the ponds, Island Pond in Præstevang near Hillerød, the colonies appear year after year in the middle of June, about one month after the unfolding of the leaves on the surface; in some summers, especially those with high temperatures, the colonies are extremely common, a single leaf often carrying many hundreds of colonies in August; in the middle of September the colonies disappear, but some of the dead tubes are to be found long after the animalcules have died. Owing to their almost black colour, they may easily be observed against the green colour of the leaves. Whereas the females of *Floscularia* and *Lacinularia* are often seen as young ones swimming freely round the colonies, this is not the case with *Melicerta* as far as I know, at all events not with *M. ringens*, which I have had most opportunity of observing. The young ones of the two first genera place themselves in the jelly, among the older mother individuals.

When the leaves reach the surface, they carry no colonies; the colonies do not appear until two or three weeks later. The resting-eggs have most probably hibernated upon the bottom whence they have risen to the surface perhaps owing to air-development and here they are caught below the large blades of the *Nymphæa* leaves. From these first colonies the others may arise, the young ones in most cases fixing themselves in or on the old colonies, in other cases in the near vicinity on the leaves. —

**Conochilus volvox** Ehrbg.

In almost all our ponds *Conochilus volvox* is extremely common. It is much more common than *C. unicornis*. In all localities a very conspicuous maximum appears during the time from 15. April to 15. May. In some smaller ponds the water may almost assume the appearance of barley-soup during this maximum. A glass of water taken from some of these ponds will contain thousands of colonies. Until the middle of June these colonies only consist of amictic females, but in June colonies are found which contain very small eggs and a little later also some resting-eggs. Then the maximum disappears, but very often amictic colonies are found during the whole year. These may give rise to smaller or larger maxima during the summer and autumn, but no mictic colonies have been found at that time. *C. volvox* is also present during winter, but as far as I know always as amictic colonies.

For some years it was incomprehensible to me how these maxima could become so extremely large in such a relatively short time. In one of the ponds, Teglgårdssø near Hillerød, one developed in June in the course of only ten days. During the study of the colonies it could often be observed that they were not always ball-shaped. It could be observed in the surface of the ball that small sectors rose above the surface; this was mainly the case with large and compact colonies. On studying these more closely, it could be seen how this sector grew larger and larger; suddenly it was pushed out of the ball, and at the same moment the sector spread out, and a new ball, not so compact as the mother ball, was formed.

It is a sort of "vegetative propagation" which takes place in this way, and it was in this way that the maxima grew so incredibly large. When a colony is laid under cover and exposed to pressure, it is seen that suddenly the colony divides into two; and that there are two balls where there was only one before. As I have made quite the same experiment with *Lascinularia socialis*, I suppose that here, too, it is in this way that new colonies appear, and all the more so since we often find either a number of small colonies round a larger one, or a large one which is almost divided in two.

**Conochiloides natans** (Seligo).

Frederiksborg Castle Lake. *C. natans* is very rare. In 1923 it was never observed, in 1924—1925 only in a few samples in May. In these samples as well as in those of June the beautiful resting-egg is often found.

Island Pond. *C. natans* was found 28/IV 1898 but only in small number. In a sample taken 3/V 1910 the species was present in incredible quantities; the plancton consisted almost entirely of it. Most of the females were mictic ones, with the resting-eggs lying in the jelly tubes. Males were very common. Already on 10/V *C. natans* had almost disappeared, but the water contained enormous numbers of resting-eggs. Neither in 1923 nor in 1924 or 1925 was a single specimen observed.

Horseshoe Pond. *C. natans* has been observed regularly immediately after the ice had disappeared, but always in small number. In 1926—27 and 28—29 as well as 29—30 I have taken samples in the openings in the ice; during the first two years *C. natans* was present and rather common. All females were amictic, but already a fortnight after the ice had disappeared, mictic females were present; a few days later the species had totally disappeared and was never observed later in the year. In our country *C. natans* is a peculiar example of a species with a very short active period, lying at a relatively low temperature.

#### **Oecistes** sp.

In one of my small ponds, Torkeri Pond, the same from which the material for my experimental studies on *Asplanchna Sieboldi* was derived, I found several *Oecistes* species on the leaves of waterplants on 11/IV 1924. During the night the pond was covered with ice and the temperature of the water during the day was only about 2° C. By 20/IV, during a period when the temperature of the water did not rise above 4—5° C., an enormous maximum of *Oecistes* developed. The alga threads were so to speak covered with *Oecistes*. Threads measuring a length of about 10 ctm., contained the species by hundreds. The animals were often united in small colonies, where 10—20 individuals sat very near each other. At the point of attachment of the foot about 10 large oblong eggs were found. In the plancton of the pond free-swimming young ones were numerous. But already eight days later after heavy and very cold rain at an air temperature of only about 2—3° C., all the coatings seemed to have disappeared. The water-level of the pond had been raised very much, the water had most probably become much diluted, and as is often the case, it was as if just this factor was able to stop a rotifer in the middle of its development. The pond was very often visited that year owing to some investigations on some Hydrachnides, but the species was never found again. It was as if external conditions were a hindrance to the development of the mictic females.

The colonies of *Conochilus volvox* and those of the other *Melicertidae*, especially those of *Lacinularia socialis*, differ from each other in some very essential points.

I have followed the maxima of *Conochilus volvox* from the moment they began to their very end. Almost always the colonies presented that peculiar phenomenon that they hardly ever contained eggs in the tubes surrounding the individuals, and that the central part of the colony was destitute of eggs of every kind. —

As already HLAVA as well as others have pointed out, *Conochilus volvox* produces young ones; the eggs are developed in the uterus; as far as I know, the same is the case with *C. unicornis*, but not with *Conochiloides natans*. Apart from

the two *Conochilus* species all other *Melicertidae* as well as all *Floscularidae* are egg-laying organisms.

In *Conochilus* it is, however, only the amictic females and the mictic females which with regard to the male sex produce young ones; the resting-eggs for a short time are deposited in the interior of the ball-shaped colony. Even the two first-named kinds of progeny may as eggs now and then be found lying outside the females in the jelly common to the whole colony. It seems to me that the amictic females, and the mictic ones with regard to the male eggs, are in reality oviparous; the extremely thin eggshell bursts at the very moment of birth. In accordance herewith we often find colonies consisting of 50—60 individuals and containing in the interior of the ball one single "summer egg".

But even the resting-eggs are hardly ever found lying free in the colonies. When the maximum is at an end, the animals contain resting-eggs. Curiously enough, I have hitherto never found colonies in which the formation of resting-eggs was a common phenomenon. I had supposed that the colonies, when the sexual periods were at an end, would have contained numerous resting-eggs, deposited in the central parts of the colony. This, however, was not the case. In the colonies only a few individuals contained resting-eggs; when they were fully developed, they were pushed out into the jelly; here they did not remain, but gliding out slowly between the single individuals of the colony they were dropped into the water. As I had supposed, the colonies were not reduced to dead ball-shaped jellymasses containing the numerous resting-eggs, deposited before the death of the individuals; the eggs drop out soon after they are pushed out of the opening of the uterus.

As far as I know, all other *Melicertidae* as well as all *Floscularidae* produce eggs and these eggs are deposited in the jelly of the colony or, if the animal is solitary, in the tube itself or in the small amount of jelly where the animal is attached to the substratum. If the colonies of the *Lacinularia* are observed, we shall find, at different seasons of the year, in some colonies the large eggs of the amictic females, in others very many small male-eggs and again in some colonies all the females carrying the large resting-eggs. The parthenogenetic eggs, have not begun the development at all when they are deposited in the jelly. I have the impression that with regard to these colonies we may often have to do with purely mictic and purely amictic colonies, but I regret that I have not had sufficient material for a more elaborate study of this question. In fig. 6, 7 Plate XIV I have given drawings of two colonies, the one containing only numerous male eggs in the jelly; in the other all the females also carry large resting-eggs. It may be supposed that amictic colonies are slowly altered into mictic ones, the amictic animals dying out and being replaced by mictic ones. —

The peculiar fact that *Conochilus volvox* in contradistinction to all other *Melicertidae* produces young ones must most probably be regarded as a peculiarity caused by adaptation to the pelagic life of the colony; the free-swimming but

always solitary species of *Melicertidae* and *Floscularidae* are all egg-producing, carrying the eggs in the jelly sheaths. It may be possible that colonies are not able to carry the heavy burden of numerous eggs in the central part of the globule, and that the free-swimming power of the colony would be dependent upon the active power of locomotion of the new-born animal from the very moment of its ejection. It seems as if the development of the young ones in *C. volvox* in the uterus of the mother animal takes place with extreme rapidity. A more thorough study of these interesting facts is highly desirable.

#### Pedalionidæ.

The family comprises the genera *Triarthra*, *Tetramastix* with *T. opoliensis* Zach. and *Pedalion*; *Tetramastix* has not been found in our country.

#### Triarthra.

Of the genus *Triarthra* we possess at all events the three species *Triarthra longiseta* Ehrbg., *T. brachiata* Rousselet and *T. breviseta* Gosse. Owing to the different length of the bristles and the position of the unpaired posterior one, three other species have been created: *T. mystacina* Ehrbg. *T. limnetica* Zach. and *T. terminalis* Plate. I have been unable to distinguish these species from each other. *T. limnetica* is in my opinion the typical limnetic form of *T. longiseta*, just as *T. mystacina* is so for very small ponds, often duck-ponds receiving fluid from dunghills. Also the species *terminalis* is in my opinion problematic, the posterior thorn being placed at different distances from the posterior part of the animal.

#### *Triarthra longiseta* Ehrbg.

Plate I, fig. 3—4. Plate XIII, fig. 7—10.

Frederiksborg Castle Lake. *T. longiseta* is most probably perennial, occurring as it does in almost all the samples all the year round; the main maximum always occurs in spring; it was very large in 1924, but rather small in 1923; from June to September it was always rare; during the autumn the number increased again. During the winter, e. g. in 1924, it was very common in all the samples taken below the ice; on 9/IV it had a very large maximum below the ice. At that time, at temperatures near zero, a very pronounced parthenogenetic propagation set in; the number of eggs carried by the amictic females did not however, exceed two; often there was only one. The mictic females did not occur before 29/IV, but the general sexual period of the colony did not begin until about 15/V. At that time *T. longiseta* was one of the main forms of the rotifer plancton, and mictic females carrying 4—5 male eggs were present in great numbers. Simultaneously very many specimens were severely infested with *Microsporidia*. The male egg carrying females preponderated by 10/V, but on 16/V most of them carried a resting-egg. This is always carried inside, it is very large, filling most of the body cavity. I have never seen the egg being laid, nor carried outside as in *Polyarthra*. In the vessels, when

the mictic females die, the resting-eggs are often found lying in the skins of the females. I am therefore inclined to suppose that they are at all events not always liberated before the death of the female. On 16/V but especially on 23/V these resting-eggs rather often lay free in the samples. When the sexual period was at an end by 29/V, the amictic females occurred in rather great number, and it is these females which now occur in different numbers during the summer months.

If plancton is taken in during the sexual period and poured into large vessels, it will be seen that the mictic females carrying resting-eggs gather on the side of the vessels turned away from the light, whereas the amictic ones and the mictic ones carrying male eggs form a milky foam at the opposite side turned towards the light. It is as if their relation to the light is altered with the development of the resting-egg. This is most probably correct, because it has been shown that the number of females carrying resting-eggs is much greater at a depth of 2—3 m than at the surface. This may be due to another reaction to the light, but it may also be because the heavy resting-eggs force the females downwards. —

Mictic females have not been observed after June. —

Asminderød Pond. *T. longiseta* is perennial. In 1922, however, it was not observed in the samples from early spring, but after the latter part of April it is probably not lacking in any sample; it seems to have a pronounced minimum from November to March. On the other hand, from the middle of March 1923 to October it was almost always numerous; the maximum may occur at very different times during the summer months; it may be divided by a summer minimum and both maxima may terminate with the appearance of mictic females; it may also appear in July and in that case, too, terminate in a sexual period. Mictic females may therefore occur at temperatures of 4—6° C. (10/IV 1923) as well as at temperatures of 20—24 (20/VII 1923).

Especially in 1923 the species had very large maxima. It seemed as if *T. longiseta*, like many other rotifers, here as well as in the other ponds, was influenced by the very severe winter of 1924, during which the ponds were frozen for about 130 days. The maxima were not great, and sexual periods only slightly developed; the number of females carrying resting-eggs was small.

Fredensborg Pond. *T. longiseta* had a large maximum in May 1922, followed by a sexual period during which almost all females carried resting-eggs. Then it almost disappeared and was always rather rare during the rest of 1922 and during 1923, most common in August 1922. Mictic females were not observed —

Island Pond. *T. longiseta* is mainly a winter and springform. —

It is rather common in December and during winter, below the ice, and immediately after its disappearance, it is one of the main forms in the plancton. The maxima may occur at temperatures very near zero, and may be due to the hatching of resting-eggs in the warm littoral zone, often with temperatures of 10—12° C. only a few inches from the ice. The mictic females appear in April; numerous individuals carry male-eggs in May, females with resting eggs are very numerous,

and resting-eggs are also found free in the samples; in the latter part of May the species almost totally disappears. —

Horseshoe Pond. The species is remarkably rare; during 1923 and 1924 it only occurred sporadically, but rather suddenly in March 1925 it had a rather large maximum, terminating in a sexual period with mictic females with resting-eggs.

Schæffergaard Pond, *T. longiseta* is most probably perennial. In July—August 1906 it had a pronounced maximum terminating in a sexual period. Then it only appeared very rarely in all the following samples till April, when a new maximum with a sexual period developed. Again it almost disappeared, but in July had a new maximum with a sexual period. Just as in Asminderød Pond we see the mictic females appear at very different seasons and temperatures: at 4—6° and at 20—24°.

In the other ponds, as Funkedam and one of the experimental ponds, *T. longiseta* only occurs sporadically, and then mainly in spring and late autumn. —

1. Wherever pond explorations have been carried out, *T. longiseta* has been found. It does not seem to occur in drying ponds or in ponds with affluxes from dunghills, sewers etc. Its home in ponds is the central part free from vegetation; it may be found in ponds rich in organic matter as well as in those with peaty, quite brownish water. —

It may be dicyclic in ponds, but often seems to be only monocyclic; the mictic females seem to occur at quite definite times of the year, and apart from these periods seem to be totally wanting, but in this respect the species differs greatly in the different ponds and also in different years in the same pond. The mictic females occur at very different seasons, at very low as well as at the highest summer temperatures.

2. The resting-eggs are extremely large in relation to the size of the females; their shape differs very much. It seems to me that it may be doubtful if they are deposited; most probably they are not freed before the death and decomposition of the mother animal. They seem to have large air spaces, but nevertheless they do not seem to be pelagic in autumn. When the sexual period is at an end, they may occasionally be found in the plancton, but then they totally disappear, being most probably deposited on the bottom. For a time I supposed that, like the *Brachionus* eggs, they were deposited upon the surface, and swept ashore from there, but I have not been able to corroborate this view. In spring the empty shells are often met with in the plancton. The airspaces are arranged in three lines over the shell; they are at that time filled with air and the shell supercompensated. I suppose now that air is developed during the embryonal development and deposited in the airspaces. In this way the eggs are raised to the surface.

3. In ponds *T. longiseta* as well as other rotifers show the peculiar phenomenon that they may almost disappear for one or two years and then, in the third year, suddenly develop a very high maximum.

4. *T. longiseta* is also an inhabitant of the pelagic region of even our largest lakes; it has been found in them all and may be regarded as perennial. Here it has almost always a rather pronounced maximum in the spring, followed by a sexual period; then it only occurs in small number, but again gets a little more common in the autumn; during winter it is always among the commonest of all the rotifers. In lakes, therefore, it is pronouncedly monocyclic with a conspicuous predilection for not too high temperatures. Here, as in ponds, amictic females continue a slow propagation between the maxima.

5. Many of the pond forms would unquestionably have been taken for *T. mystacina* Ehrbg. by previous observers; that there is an enormous difference especially between these forms and those from our largest lakes (*T. limnetica* Zach.) with regard to the length of the thorns is beyond all doubt; *Triarthra* from ponds have often thorns only half as long as those from the pelagic region of lakes; on the other hand I have in Fjenneslev pond at a depth of only 1 dcm. found a *Triarthra* whose thorns were  $3\frac{1}{2}$  times as long as the body. Being unable to find other more valuable characters, I have not tried to keep these forms distinct.

#### ***T. brachiata* Rousselet.**

Plate XIII, fig. 5—6.

*T. brachiata* is not rare during the first part of the summer in the central part of small ponds free from all vegetation. This species, too, is a very slow swimmer; The species was found in July 1929 in a little pond in Bistrup near the borders of Furesø. It had a great maximum in the last part of June and in August; then it totally disappeared and was not found in a single specimen in any of the autumn samples. The sexual period occurred in August. The resting-egg is very large and fills almost the whole body cavity of the female. It seems as if it also has air spaces, but hitherto it has not been found floating in the water. —

#### ***Triarthra breviseta* Gosse.**

*T. breviseta* has a rather peculiar occurrence; it is pretty rare, but in all those ponds in which it has been observed it has been found in the latter part of November, appearing suddenly at a temperature of about 6—8° C. Very often the ponds are then frozen for a week or more, but when the ice thaws again in the beginning of December, the females all carry large resting-eggs. The species may then have a large maximum, being one of the main forms in the scarce pond plancton. When the ponds freeze again and do not thaw until April, the species has disappeared; then the resting eggs are hatched and a new maximum appears in April at 8—12° C. During the summer I have not met with it.

#### ***Pedalion mirum* Hudson.**

*P. mirum* has been found in Fredensborg Pond, Horseshoe Pond, Nøddebo Pond, Funke Pond, Island Pond and the M. pond of my experi-



mental ponds. It has always been found sporadically and always in the summer months; it was fairly common only in M. pond. It was found in M. pond on 3/VI 1900, and disappeared again on 18/IX. The maximum set in on 27/VI and was relatively large in July; then an enormous *Dinobryum* maximum began, during which the water was coloured yellowish and the plancton net filled with thick gelatinous matter, during which almost all other plancton organisms, also *Pedalion*, seemed to disappear. When the maximum ceased, *Pedalion* became more common again. Mictic females with numerous male eggs appeared on 10/IX and 18/IX, resting-eggs were found free in the sample. Then the species totally disappeared. —

During pond explorations in different parts of the country *Pedalion mirum* has often been observed. It is a pronounced summer form, always occurring in the first part of June; it has its maximum when the highest temperature has been passed, and its sexual period in September. The maximum is never very large. It usually disappears entirely in September—October. In some localities, e. g. some of the Hellebæk ponds, it has been found as late as November, being then only represented by large eggless amictic females. — As a rule the species rests as resting-eggs from October to the beginning of May when the resting-eggs may be hatched. Owing to the propagation of the amictic females, the maximum is developed, whereupon the mictic females occur.

Their occurrence is restricted to only a few weeks, and in most localities the species then entirely disappears.

It has never been found in the pelagic region of lakes, nor in drying ponds. Its home is the central parts of ponds which are either quite free from vegetation or have a broad zone of *Potamogeton natans* near the shore. It seems to be fond of peaty water; there it may often have a deep yellow colour and may especially at high temperatures have very beautiful red and blue colours. I forgot to observe whether they were restricted to the mictic females. Now and then *Pedalion* has been found in bog holes which were only some square meters large. —

The mictic females carry the male eggs in clusters of 10—12, and the males then arrive in great numbers; in the lighted borders of the vessels, in which were plancton samples containing thousands of *Pedalion*, males appeared abundantly.

The mictic females carrying the male eggs are commonly somewhat smaller than the amictic ones. MONTET (1915 p. 346) made the same observation; he states their size at 150—156  $\mu$ . The females carrying the resting eggs are much larger, about 170—180  $\mu$  or more. As far as we know (MONTET 1915 p. 350) the females only carry the resting eggs a very short time; it is doubtful whether they are agglutinated to algæ or sink to the bottom.

#### Pterodinidæ

contain the two genera *Pterodina* and *Pompholyx*.

### Pterodina.

The *Pterodina* species are pronounced pond forms which have never been found in the pelagic region of larger lakes, nor in the central parts of smaller lakes or ponds. As is well known, some of them are commensalists and semiparasites on *Asellidae*, *Astacus* a. o. Most of them are pronounced bottom forms, and as such difficult to get in great numbers. Some species belong to the *Potamogeton* zone of our largest lakes, living at the surface on the long garlands of *Ceratophyllum* and *Myriophyllum* (Esrom Lake 15/IX 1929). Most of the species I have found at all seasons of the year, but I have the impression that their maxima occur mainly at low temperatures. Of *P. patina* a remarkably high maximum was found in the latter part of November in a little pond without vegetation, but with the bottom covered by decaying leaves. A sexual period is quite unknown, and males have only rarely been observed (W-L. 1923 p. 287).

### Pomholyx.

Of the two species *P. complanata* Gosse is a true pond form, a pronounced summer form belonging to the central parts of smaller lakes and ponds. Sexual periods have not been observed.

#### *P. sulcata* Gosse.

Frederiksborg Castle Lake. The species appears here in the middle of June at a temperature of 16°. At this temperature the huge masses of resting-eggs scattered over the lake bottom may be hatched. The maximum arrives rather suddenly and always at the highest summer temperature. It is very short, lasting no more than 10—14 days (commonly 27/VII—19/VIII), at that time the species had an extremely high maximum. Simultaneously the sexual period set in, very many specimens carrying male eggs, the number of which never exceeded four; most commonly it was only three. The lighted side of the vessel teemed with clouds of the species; when a drop was brought under the microscope, the specimens arranged themselves in a long series all turning the wheel-organ towards the lighted side. The males swam in front of the females, whirled round by their wheel-organs, and during this motion going so to say from hand to hand, arriving in the whirling stream from one female as soon as it had safely got away from another. In these days incredible numbers of males were hatched; four or five days later not a single male could be observed. — Immediately afterwards the females carry the ball-shaped resting-egg, characterized by its double contours. It is soon dropped off; the maximum terminates before the end of August and only a small number is left in November.

The period of the mictic females does not last more than about a fortnight.

In several of the other ponds, e. g. Asminderød Pond, Funke Pond and

Schæffergaards Pond, the species had also a large maximum; everywhere it appeared in June and disappeared in November with maxima at the highest temperature; further, it is a regular plancton organism, found in the pelagic region of all our lakes and there, too, with a maximum at the highest summer temperature. Mictic females were observed in Skanderborg Lake on 30/VII 1902, temperature 14.

### Floscularidæ.

Owing to the manner in which I have studied the microscopical life in our ponds and lakes I have only very few and fugitive observations relating to all sessile rotifers. The *Floscularidæ* seem to be pronounced summer forms; on this point, as far as I know, I agree with almost all observers. As far as I have hitherto seen, they all form the elegant resting-eggs in September—October, whereupon they disappear. *Stephanoceros* has only been observed a few times; *Apsilus* never. In summer *Floscularia algicola* Huds. is common in the coatings of *Gloiothrichia* on the stones in the littoral region of our larger lakes.

In the pelagic region of lakes and ponds there occur three free-swimming *Floscularia* species, *F. libera* Zacharias, *F. mutabilis* Bolton, and *F. pelagica* Rousselet. In 1904 (p. 149) I maintained that *F. libera* was a typical summer rotifer in the pelagic region of many of our lakes; at that time the two other species had not been found; later on *F. mutabilis* was found in several ponds; it is mainly a summer form, but it may be found as late as October—November. ZACHARIAS, too, (1899, p. 65) says that he has seen it in the winter. *Floscularia pelagica* was found as a conspicuous part of the summer plancton in the little lake Klaresø near Hellebæk, North Seeland. It appeared in July and had disappeared in October; the jelly tube is of an extremely elegant, elongated form, hyaline as the purest water, and therefore difficult to observe. The animals swim with the hindpart of the tube directed forward. In the tubes lie the female eggs as well as the much smaller and more numerous male eggs.

Owing to an accident, I failed to get the males and the resting-eggs. A plancton mainly consisting of this very aberrant form leaves a very peculiar impression.

To my great astonishment in May 1923 I found, upon the roots of beeches hanging down in the water in Horseshoe Pond, rich coatings of several *Floscularia* species; already in June they had entirely disappeared and in the following years these coatings were not found again; the main forms were *F. proboscidea* Ehrbg. and *F. cornuta* Dobie; of the last-named mictic females were often found; immediately before the disappearance of the *Floscularia* heavy rains diluted the water considerably.

### Bdelloida.

As is well known, the *Bdelloida* are regarded as totally acyclic; males have never been found. In the moss-inhabiting species resting-eggs have been observed (JANSON

1893) but whether these resting-eggs are comparable with those of the other Rotifera and the result of a mating-process, is a matter of doubt. My knowledge of this group is but small. As is well known, many of the species will tolerate even very low temperatures.

On an excursion in November to the lake at Frederiksborg Castle I found the roots of some chestnut trees covered with a coating of *Stentor*, *Brachionus urceolaris* and *Philodinidae*. With other purposes in mind the locality was visited regularly during the whole of 1921—1922, and it was observed that the whole winter the *Philodinidae* were present in almost incredible numbers also below the ice; in spring when the ice thawed, they were still present but not so common, and during the summer they almost entirely disappeared; this was also the case with *B. Bakeri* and *Stentor*.

As far as I know, no one has hitherto pointed out this almost incredible winter maximum in the Bdelloida, which is sharply defined and during the rest of the year displaced by a minimum just as pronounced as the maximum in winter. As sexual periods and maxima coincide in so many cases, I had hoped that this time I should really be able to give some information with regard to the sexual periods, also in this group of rotifers. With great hesitation I venture to remark, that twice I saw among the thousands of *Philodinidae* (*Rotifer vulgaris*) a little creature, unquestionably a rotifer male, with a ciliary wreath resembling that of *Rhinops*, but without any projecting rostrum, shaped like a *Rhinops* male and with two red eyespots at rather a long distance from each other. The male was new to me, but both times I failed to get it isolated. It moved round and between the numerous females with extreme rapidity. If we know little with regard to the periodicity of Bdelloida in nature, we owe it to the paper of DOBERS and others that we are remarkably well informed with regard to their life in cultures.

A few Bdelloida occur in the plancton; among these are the most elongated of all Bdelloida *Actinurus neptunius* Ehrbg., which already ZACHARIAS (1900 p. 463) found as a plancton organism near Lübeck, and some rotifer species, especially *R. macroceros* Gosse and *R. macrurus* Ehrbg. In my area of exploration, I have fairly often found *Actinurus* as a true pelagic inhabitant of ponds and larger bogs. In the pelagic region it is always a summer form; the maximum lies in August—October; it was large in Fredensborg Castle pond; in some ponds it is very common. When the animal swims, all the segments are telescopically withdrawn into each other. When the sample with the living organisms is poured into the vessel, the animals first lie like long stiff rods at the bottom of the vessel; later on they unfurl the wheel-organ and swim away at a great speed. I have never seen eggs attached to the body. As far as I know, these pelagic *Actinuri* have never been subjected to a more thorough examination. To my mind, it is doubtful whether we here have to do with the typical *A. neptunius*. In some of my experimental ponds especially *Rotifer macroceros* Gosse appears occasionally, but always in a relatively small number.

## Postscript.

**Brachionus pala in Bistrup Pond in 1930.**

Plate V, fig. 20—38.

As mentioned p. 115, samples were taken every fortnight during the winter-months of 1930. The pond was frozen only for three weeks in the latter part of January and in the beginning of February. *Brachionus pala* did not appear before 2/V; at that time it was only present in very small number, all the females were amictic and all were of the typical *pala* form without posterior thorns. The form was an extremely small form. By 15/V *B. pala* was more common but in form and size did not differ from that of 2/V. This early spring form was identical with that with which we had become acquainted on 20/IX (fig. 19), the last time we met with the species in 1929. Also on 20/V and 31/V the species was only present as the typical *pala* form without the slightest indication of posterior thorns; the species was, however, increasing in number and from 15/V mainly mictic females were present; on 15/V most of them carried male eggs, and already on 20/V a few very large females were observed (fig. 22); on 31/V many also carried resting-eggs; their size had increased. On 7/VI it was present in enormous numbers; the sample was coloured milky with the millions of animals. The majority were amictic females, almost all of the typical *pala* form; but now a few specimens with posterior thorns had appeared; these all had amictic eggs. On 16/VI conditions were almost unaltered; the number of specimens was still enormous, most of them belonged to the type *pala*, perhaps a few more to the type *amphiceros* with short posterior thorns (fig. 30). On 24/VI the great change took place (fig. 31—36); the maximum was still very large; the typical *pala* form had now almost disappeared (fig. 31); a good many with very short posterior thorns were present and the number with well developed posterior thorns predominated (fig. 34). The different forms carried all three kinds of eggs. One of the type *amphiceros* but with very short thorns (fig. 35 a) was isolated; it carried a large amictic egg with an almost fully developed embryo; the female was observed under the microscope, and the birth of the young one seen. Shortly after birth the size of the young one increased enormously and half an hour after birth the young one was drawn (fig. 36 b). It will be seen, that the posterior thorns of the young one is twice as long as that of the mother animal. Now a study of the sample showed that it contained very many young ones, very hyaline, small animals with a very soft wrinkled skin and long posterior thorns; unquestionably born by typical *pala* mothers or mothers with very short posterior thorns. On 3/VII all the small typical *pala* forms had disappeared. The maximum which was still very large was now formed by the very large *amphiceros* forms (fig. 37—38) with very long thorns; these forms carried all three kinds of eggs and many carried resting-eggs. The two figures 37, 38 show a long thorned animal, in fig. 38 when

swimming in fig. 37 when dead (see p. 115). We have now in samples gathered upon 20 excursions during the year 1929—1930 studied the seasonal variation of a particular colony of *B. pala*.

We have seen how a typical forma *amphicerus* with extremely long thorns during the period 22/VII to 2/VIII 1929 was altered into a form with very short thorns which again on 22/VIII had been altered into the typical *pala* form without any thorns at all. As such it totally disappeared from the plancton. Again on 15/V it appeared in the same form as *B. pala*. As such it developed its enormous maximum in the latter part of May and had its sexual period. On 7/VI extremely few *amphicerus* forms were present but only nine days later on 16/VI the great change had occurred, almost all specimens being of the typical *amphicerus* form. Here it has been clearly shown that long-thorned forms are hatched from eggs carried by very short-thorned mothers. The excessive length of thorns occurs during the period 24/VI to 3/VII.

There is now no longer any doubt that here we have to do with a form series; in autumn the typical *pala* form is developed from eggs carried by long-thorned mothers, and in spring thorned animals are developed from eggs carried by very short-thorned mothers.

The great change takes place in the course most probably of eight days, at all events in not more than nine to ten days.

The periodicity of *B. pala* in Bistrup pond in 1929—30 is given in the following list.

Tp. 21	20	18	17	14	9.5	5	6	4.5	1
22/VII	21/VIII	22/VIII	20/IX	5/X	24/X	16/XI	3/XII	8/I	1/II
cc	c	c	rr	0	0	0	0	0	0
Tp. 3	9	12	15	15	21	21	22	21	23
20/III	12/IV	2/V	15/V	20/V	31/V	7/6	16/VI	24/VI	3/VII
0	0	rr	+	+	cc	ccc	ccc	ccc	ccc

Having now observed this seasonal variation through two consecutive years, it seems as if this colony as well as several others belonging to small very shallow highly eutrophic ponds is subject to a very characteristic seasonal variation. If we keep in mind that numerous colonies of *B. pala*, also those belonging to eutrophic ponds, do not show the slightest trace of a seasonal variation, and never seem to pass into an *amphicerus* stage, it may be supposed that external conditions alone cannot cause the seasonal variation. On the other hand, when we see that the seasonal variation always sets in in May, that it attains its highest development at the highest temperature and that the colony returns to the typical *pala* form in September and is only present as such during the winter, there cannot be any doubt that external conditions must have some influence here.

This holds good especially if we remember that the excessive development of the posterior thorns has hitherto only been observed in colonies with a periodicity very aberrant from that which we commonly find in *B. pala*. Whereas the typical *B. pala* is commonly perennial, or at all events often dicyclic, with large maxima in autumn and spring, the colonies with excessive development of the posterior thorns are typical summer forms which only seem to have their maxima at the highest temperature, do not appear before the middle of May, and disappear already in September. The observations relating to those colonies of *A. Sieboldi* which developed the most aberrant humped forms are seen to give a similar result. — The observations in Fjenneslev Pond and Bistrup Pond seem to show that there may perhaps be a connection between periodicity and excessive form variation, furthermore that colonies with a peculiar life and peculiar seasonal variations may perhaps give rise to genotypically stamped "petites espèces". That this may have some connection with the great variations in temperature and all factors combined with it, is beyond all doubt; how significant this connection is we do not know; and it must be remembered that in very many localities similar to Bistrup and Fjenneslev Ponds we find colonies which show no seasonal variation at all. The periodicity of these colonies we do not know. What still remains is to take colonies of the Bistrup type and the common one into the laboratory and at the moment when the great variations take place, work with the colonies experimentally. This I hope will be done next year. —

### General Remarks.

In the following I shall try to summarize the results of my own investigations with regard to the periodicity, sexual biology, and cyclomorphoses of the Rotifera.

### The Cycles.

At a first glance it would seem rather peculiar, but in reality it is very intelligible, that studies in nature relating to the cycles of the Rotifera furnish the least valuable results for the very groups, for which laboratory studies yield the most trustworthy results. Laboratory studies have mainly been carried out with members of the fam. *Notommatidae* and other bottom rotifers further with rotifers from very small ponds, outdoor studies mainly with free-swimming rotifers and real plancton organisms. In both cases the choice of subjects is intelligible and almost dictated by the mode of investigation. It is much easier to accustom bottom organisms to laboratory conditions than plancton organisms; the results gained in the laboratory from the first-named group are therefore commonly more valuable than those gained from plancton organisms. When furthermore studies in nature were almost

solely directed towards plancton rotifers, this phenomenon has in the first place a historical basis, inasmuch as studies relating to the cycles, the cyclomorphoses and the sex-determination of rotifers as well as Cladocera in some respects are the offspring of the plancton studies. Furthermore outdoor explorations have in numerous cases showed that it is almost impossible to find that regularity with regard to life conditions, seasonal occurrence, and sexual periods which is so highly characteristic of many plancton organisms, and which is the *conditio sine qua non* if organisms are to be used for the study of the above-named problems. This regularity is, so to speak, a plancton character, in very many cases increasing with the degree in which the species have emancipated themselves from a substratum and become altered into free-swimming organisms in the water-layers above the bottom. That this regularity exists is really very intelligible.

It is as if the extremely varying external conditions characterizing the home of many bottom rotifers, especially those living in very small water volumes with extremely strong variations in temperature, chemical composition caused by dilution owing to sudden downpour, or total desiccation caused by drought periods, have influenced their life periods and given them the stamp of irregularity. The animal society of ponds and smaller water-basins are forced to live their life in accordance herewith, and the study of these organisms must be carried out so to speak in accordance with the principle never to put off to to morrow what you can do today. I for my part am now inclined to refer the forms for propagation of the Rotifera to five different types partly dependent upon habitat; investigations carried out in other latitudes may perhaps bring others to light.

1. The *Hydatina* type. Habitat: drying pools. Of all the different types of small waters the temporary pools which only get water from melting snow and are desiccated as a rule before the middle of May, in reality offer their inhabitants the most stable life conditions. The predominant feature of these is that life in the active stage is only possible in them from the moment they are thawed to the moment of total desiccation; in our latitudes this period is always in spring and commonly only lasts for five or six weeks. Among these pools I have mainly studied the life in those which get manure from stables and soil; rotifer life in the temporary pools of the meadows is not quite unknown to me. As far as I can see, apart from the differences in the chemical composition of the medium, their life conditions do not differ very much from those of manure pools. The main form of the manure pools is *Hydatina*. Its life history exactly reflects the life conditions this habitat is able to offer. When the resting-eggs are hatched in early spring the amictic females in the course of a few weeks fill the water with myriads, these myriads produce mictic females which in the course of a few days produce about 50 males each which are immediately ready to pair. After a few days the resting-eggs are developed, and a week later the whole colony only exists as resting-eggs which remain in the bottom material for about 10 months. The life of the colony



in the active stage does not last 4—6 weeks. Amictic females ready to continue the development after the sexual period do not exist, or are as a rule rare. Now the outdoor investigations show the very interesting fact that even if *Hydatina* lives in a locality which has water the whole year round, or the year is a very wet year, in which all generally desiccating ponds are waterfilled as an exception, nevertheless the colonies die out. The colonies are biologically adapted to the ordinary environmental life conditions, and cannot tolerate exceptional conditions, which as a matter of fact, would expose them to the greatest specific dangers.

When it has been shown by laboratory studies that under homogeneous life conditions in the laboratory *Hydatina* may propagate parthenogenetically in uninterrupted succession for 2½ year (more than 500 generations), these results are of the greatest interest in many respects. On the other hand, it is of no less interest that the life of *Hydatina* under natural conditions is ruled by quite different and very fixed laws. The outdoor investigations show that strictly speaking the results gained in the laboratories with regard to the life history of *Hydatina* are all pathological. — Laboratory studies may increase our knowledge of the extreme conditions under which an organism may live its life and of their influence on special physiological processes, e. g. their influence on the ovarium and the vitellarium, which causes variation in the size of the egg. On the other hand, they can only give us hints as to what life is like under natural conditions. PUNNET'S pointing out of special strains, corroborated by many recent authors, clearly shows that even under laboratory conditions the physiological peculiarities of the explored line cannot be totally suppressed. In other words, environmental conditions through accumulation really have stamped the behaviour of the organisms and with that in an invisible way even the soma.

Furthermore, I cannot see better than that the appearance of mictic females among organisms like *Hydatina* is really under normal life conditions limited to distinct generations, commonly the second or third generation after the resting-egg; that under quite abnormal conditions they may appear in amictic generations far removed from the resting-eggs and in a number which is never reached in nature is a matter merely of special interest.

Combined laboratory and outdoor investigations would seem to show that the colonies, in the middle of their life time, are in a labile period in which external conditions may influence the propagation, and this period intervenes between periods during which this is not the case; during the first the propagation is invariably amictic; no one has been able to hatch a mictic female from a resting-egg; and normally the second generation is also amictic. In the last part of the lifetime, here with regard to *Hydatina*, almost all females are normally mictic, and it is only with difficulty possible for conditions in nature to compel the line to amictic propagation.

2. The *Rhinops* type. Habitat: permanent small ponds with or without a free central "pelagic" zone whose depths are below one metre or only a few metres.

Here we find those rotifer communities which, at all events in our latitudes, exhibit the greatest variation with regard to all biological and morphological phenomena. These great variations are in full accordance with the habitat. It is just these ponds which are subject to the greatest variations with regard to the period of freezing, desiccation, temperature, chemical composition especially as to hydrogen ion concentration, amount of O, CaO and amount of organic matter.

How differently these rotifer-communities of permanent ponds behave common to most of them is a sexual period in spring similar to that of *Hydatina*. In these ponds we find some rotifers which almost everywhere seem to behave quite like *Hydatina* with regard to their propagation. In spite of the fact that the water level is almost the same the whole year round, they disappear at the same time as *Hydatina*, their active life being restricted to only about 4—6 weeks; all the other weeks of the year are passed in the resting stage. *Rhinops vitrea*, related to *Hydatina* belongs especially to this category. It is very regrettable that we have not the slightest knowledge with regard to *Notops brachionus*, the nearest relation of these two genera. It has never been found in our country.

*Conochiloides natans* belongs to the same category, at all events in many localities of our latitudes. With regard to these species, too, I cannot see better than that the appearance of the mictic females is mainly limited to definite generations, beginning with the second and third after the resting-egg.

Parallel with these forms are those which may in many localities behave quite like *Hydatina*, *Rhinops* and *Conochiloides*, also disappearing 4—6 weeks after the first resting-eggs have been hatched, these being hatched immediately after the melting of the ice. To these forms belong in the first place upon some localities *Asplanchna Sieboldi* and in a good many localities also *Brachionus pala*. —

It is, however, a characteristic feature of the same species that in numerous localities they do not disappear totally after the sexual period but occur in a small number active in the water-layers. In other words, this means that after the production of mictic females during the spring, some amictic females have continued the development of eggs, giving rise to amictic females, which uninterruptedly produce new amictic generations.

It is the rate and power of propagation in these amictic summer and autumn generations which varies from pond to pond and from year to year, which puzzles the observer and makes it impossible for anybody to prophesy anything with regard to the propagation of all these species. In our country colonies which have a pronounced spring maximum followed by a sexual period, hardly ever give rise to greater maxima or sexual periods later in the year.

It is characteristic of all these species that even if the environment seems no hindrance to continued active life, nevertheless, in very many localities it may be brought to an end with extreme abruptness. —

Sudden variations in the chemico-physical conditions of the environment may in the course of eight days cause the total extermination of the species in the

water-layers, on the other hand that it always should be variations in external conditions which should cause the extermination of the colony, seems improbable to me. The phenomena are equally observable in ponds with and without water bloom phenomena, and differing from each other by great variations in pH; I do not venture upon any more thorough classification of rotifer life in these ponds.

3. The *Anuræa* type. Habitat: permanent ponds, especially the central parts free from vegetation and the pelagic region of larger lakes.

From the above-named forms among which the amictic females play a rather inconspicuous rôle after a sexual period, we come to forms abounding in these, even after that period. They continue amictic propagation the whole year round; now and then, at almost all seasons of the year; they give rise to considerable maxima and sexual periods. These occur at different periods in the different years, and at very different times in the different localities.

The main forms of this group are *Polyarthra platyptera*, *Triarthra longiseta*, *Anuræa aculeata*, *A. cochlearis*, *Brachionus pala* in many localities, *B. angularis*, *Asplanchna priodonta*; they all belong to the so-called perennial rotifers; commonly they have a sexual period in April—May, but this may be wanting, they may appear and disappear quite irregularly. The amictic females may produce their young ones (*Asplanchna*) or their eggs at temperatures near zero as well as at the highest summer temperatures; at both these extreme temperatures the propagation is commonly very slow but, on the other hand, now and then great maxima appear also at both temperatures, though mainly during the summer. Sexual periods, i. e. the production of mictic females, may be observed at the highest summer temperature and at all events in November at temperatures of 6—8° C. Some of these species are to be found in water of every kind, eutrophic ponds, and ponds with pH about 4.5 as well as about 9. It would seem, however, that at all events *Brachionus* avoids ponds with low pH, though the *Anuræa* do not.

When we remember the enormous environmental variations to which the different colonies are subject in their enormous area of distribution, it is, in my opinion, highly improbable that the appearance of mictic females in a line should primarily be dependent on these annual variations in the locality where they live. The habitat of all these species is partly ponds partly pond lakes and lakes.

4. *Pedalion* type. Habitat: The central vegetation-free zone of rather small permanent ponds and pond lakes. A rather small but very interesting group of rotifers is the one to which the stenothermic summer forms belong. They do not appear before the temperature is 12—14° C., and have their maxima at the highest summer temperature. The maxima are followed by a sexual period, and then the species disappear in the autumn almost at the same temperature at which they appeared in spring. *Asplanchna Sieboldi*, *A. amphora*, *Pedalion mirum*, *Pompholyx sulcata*, *Gastropus stylifer*, *Ploesoma Hudsoni*, the pelagic *Rattulus*-species, *Anuræopsis hypelasma* belong to this group, also the aberrant colonies, especially of *B. pala*, mentioned under 3. All these species live either in the central parts of ponds free from

vegetation or they are real plancton organisms in pond lakes. It is highly probable that many of the benthonic rotifers belong to the same category but of that we know nothing.

It is characteristic of all these species, in the first place, that the resting-eggs require for their development the environmental conditions which prevail in May—June, not those of April—May. The truth is most probably that the eggs of many of these species living in the central parts of the ponds and lakes are deposited not at the shore where the higher temperatures in early spring are developed but at the bottom of ponds and lakes and where temperatures of 12—16° C. do not reach the locality where the eggs are deposited until one or two months later than in the littoral zone where the eggs of most of the other rotifers are deposited. I am inclined to suppose that it is the higher temperatures which the resting eggs of these summer forms require. This may be correct, on the other hand it must be remembered that the resting eggs of *Hydatina* which are deposited in the littoral region during the first sunny days for a few hours may also be exposed to temperatures very near 12—14° C.

Further, it is characteristic of the group that the amictic females often produce enormous maxima in an extremely short time owing to their great power of reproduction at the highest temperature of the water. This is quite the opposite of relations in groups 2 and 3, where the rate of production by the amictic females at the highest summer temperature is but small.

Owing to the enormous amictic reproduction huge, but often very short, maxima occur. During these the said forms may for a period of a week be the main planctons. Then the mictic females appear and the water teems with males; resting eggs are formed, and the period comes to an end, commonly before the beginning of September. Amictic females may continue a slow propagation in October, but long before winter sets in, the species exist only as resting eggs. —

Nearly connected with this group are those very few rotifer species whose maxima seem to be developed at very low temperatures, only a few degrees above zero. To this group belong especially some *Notholca* species but perhaps also some others especially species belonging to the *Bdelloida*, the *Notommatidae* and *Pterodinadae*, further *Oecistes* species (p. 177), *Triarthra breviseta* (p. 177) a. o.

In many respects the life of this group is in accordance with that of the *Hydatina* group, the main difference between the two sections being that the resting eggs are hatched at different seasons of the year. —

5. As a fifth group may be mentioned the acyclic one. It is questionable whether it is a natural one. It includes all the *Bdelloida*, most probably some of the *Notommatidae* and species of the genus *Lecane*, furthermore some lines (clones) of pelagic rotifers living in the pelagic region of our largest lakes.

At the beginning of the investigations it seemed natural to divide the rotifers into polycyclic, dicyclic, monocyclic and acyclic forms. In reality this division is of very little value. There is no doubt that numerous rotifers are polycyclic in some localities and in some years in others di- or monocyclic and even acyclic (*Anuraea*). Even if *Hydatina* and *Ploesoma Hudsoni* are both monocyclic, their life is nevertheless quite different, since they belong to localities where conditions are very different. Here as everywhere else, more thorough investigations show that classifications and divisions may have their significance at the beginning but as the investigation proceeds it will almost always become evident that the biology of the organisms cannot be pressed into schematic groups.

If, with regard to the two female forms, we combine the results of the laboratory and the outdoor investigations, we arrive at the highly remarkable result that the amictic females are predominant in all the above-named five groups.

The amictic females but never the mictic ones may often pass 10 months of the year in the resting-egg stages; in all groups they create the huge maxima and their lifetime is longest. In the life of the species the rôle of the amictic females is to augment the number of specimens which derive from a single egg-cell. Without power of bisexual propagation their rôle during the last part of the great maxima is to produce the female sexual forms; the male ones they cannot produce; this duty is assigned to the female sexual forms themselves.

On the other hand the period in which the mictic females occur does not last more than about two or three weeks; they themselves are never able to create the maxima, and rarely to increase them, and they never live a latent life as resting eggs. By themselves they are unable to uphold the species; they by themselves have no power to produce other than male progeny, their power to produce female progeny being dependent upon fecundation.

It is very interesting to see that fecundation of the mictic females not only alters the sex, but that fecundation also totally alters the structure of the egg-shell. This is, in all male eggs, as far as we know, only an extremely thin very hyaline membrane, in the fecundated male egg, i. e. the resting-egg, it has a for almost every species highly characteristic egg-shell. — I think there can be no doubt that this egg-shell must be prepared by the female, in other words that fecundation also influences the somatic cells of the female.

If we further remember that the life of the mictic females of *Asplanchna Brightwelli* is only about 12—14 days, and that the same female before fecundation lays male eggs, after fecundation resting-eggs, it seems that the time in which fecundation makes its influence felt upon the somatic cells of the female must be extremely short, incredibly short in comparison with the extremely complicated structure of the shell. A combined cytological-physiological study of these problems would perhaps give results which would have a much wider bearing than the mere elucidation of this special point in the biology of the Rotifera. In this connection it would perhaps be of interest to these particular phenomena that we

occasionally find eggs which are unquestionably resting-eggs, but where the shells are not fully differentiated like those of typical resting-eggs (*Asplanchna*).

The physiology of propagation of the mictic females differs very much from that of the amictic females. They produce the male eggs much faster than the amictic ones the female eggs; the amount of yolk mass present at a given moment is distributed simultaneously over the total amount of male eggs. This, together with the fact that the males get no time through active life to reach the size of the females, causes the reduction of the male sex. Their organism is adapted to create in the shortest possible time a superabundance of the male sex ready to fecundate the mictic material of females, or if necessary (or casually) the mother animal itself.

In my eyes the amictic females are only the same as, and in every regard comparable with, the sporocysts of the Trematoda, a comparison which is very natural to everybody who, in the Turbellaria, the offspring of the Trematoda, see the nearest relations of the Rotifera. They are free-swimming sporocysts; they have the same destination as these: parthenogenetically to augment the amount of specimens derived from a single egg-cell. Only they have not been recognized as such, because, owing to their active and not parasitic life, morphologically they are not distinguishable from the sexual females. It is the parasitic life of the Trematoda, the development of the sexually ripe animals through a stage, first of parasitism (*Cercaria*) and later of latency (Cyst) which has made it difficult to see the similarity.

### Cyclomorphoses.

As often mentioned above, there is no doubt that the plancton rotifers are subject to a very pronounced local and seasonal variation; it is most pronounced among the perennial rotifers, not so conspicuous in the periodic ones; and similar phenomena are unknown among the bottom rotifers.

Whereas the seasonal variations in the plancton Cladocera may in very many cases be in accordance with the buoyancy theory, and at all events cannot so far be interpreted on any other theory, this is much less the case with regard to the Rotifera.

The adversaries of the buoyancy theory have therefore often used the seasonal variations of the Rotifera as a weapon against it, in my opinion quite unjustly. They have not remembered what the advancers of the buoyancy theory have again and again maintained, viz. that the organisms may respond to the claims from without with regard to greater power of buoyancy in a very different manner and by no means always by variations in form: (W-L. 1923). Furthermore, they have no clear conception of the fact that the seasonal variations in temperature, and all the factors combined with them (variations in viscosity and specific gravity), have quite another material to work upon with regard to the Rotifera than with regard to the Cladocera. A brief consideration will presumably show that in reality

it is intelligible that, if the Rotifera should react to the above named seasonal variations in the external medium, it could not in the first place be by means of form variations, and that all that at the first glance looks like seasonal variations cannot in fact be interpreted solely in that way.

1. We know firstly that the two kinds of propagation, uni- and bisexual among the Cladocera are bound to the same female. The same specimen may begin parthenogenetic propagation, form resting-eggs when fecundated, and then again fall back to parthenogenetic propagation. Among the Rotifera we find two kinds of females, the amictic and the mictic ones. Upon the first named fecundation has no influence; it is the main form; the mictic one is only present once or twice a year and only for a few weeks, often only for a few days. In several localities, it seems that it does not appear every year.

The amictic females will, quite like the Cladocera, fill the waters with new broods generation after generations and these generations will be exposed to quite the same seasonal variations in the external medium which have caused the cyclo-morphoses among the Cladocera. But whereas these variations in the Cladocera may be directly induced into the resting-egg, in the Rotifera this will only be possible in a round-about way, namely through the mictic female. Therefore, as far as I can see, the possibility of inherited variations through accumulation of small modifications is smaller in the Rotifera than in the Cladocera.

2. As is well known, we find among the Cladocera a care of the progeny derived from the parthenogenetic eggs, which are developed in a breeding pouch and nourished by fluids from the mother animal.

With regard to the Cladocera we know that, during early summer, the young ones of the *Hyalodaphnias* are born with higher helmets than those possessed by the mother animals when they were born; it is this phenomenon which has been called pre-induction. It cannot be understood in any other way than that the regular variations in the external medium have been introduced through the mother organism into the brood. The result is that the brood is born better adapted to a lesser bearing power and lesser viscosity of the freshwater than the mother organisms. In the Rotifera as a rule we see nothing of all this. Most of the rotifers, even many plancton rotifers, deposit their eggs; most of the plancton rotifers carry the eggs outside the body and they are commonly hatched at summer temperatures in the course of about twenty-four hours. Only very few produce young ones (*Asplanchna*, *Rhinops*); and in one of these very genera, *Asplanchna*, we have seasonal variations, which may perhaps best of all be compared with the seasonal variations of the Cladocera. It seems to me that the possibility of an influence on the part of the external medium during the embryonal development must be greater in the Cladocera than in the rotifers. It must be greater in the group where the development takes longest and where the variations in temperature causing variation in the number of strokes of the legs which again causes variation of

food supply, have the longest time to influence the amount of food supply to the mother organism and from it the development of the offspring.

3. It is furthermore an established fact that the Cladocera pass through a long series of moults; furthermore, that the buoyancy organs of the perennial Plancton-Cladocera at rising temperatures as a rule increase in length from moult to moult during the spring while they are reduced during the autumn; the helms of the *Hyalodaphnias* are augmented disproportionately during the spring in relation to the length of the valves, in the autumn, at falling temperatures, they diminish without any corresponding diminution of the valves. This phenomenon can only be interpreted to mean that the regular variations in the external medium influence the mother animal, and that simultaneously with their influence on the offspring during the embryonic development; the influence on mother and child takes place in the same direction. —

In the rotifers we see nothing of all this; moults do not take place; all earlier suppositions to that effect are most probably wrong; they may be referred to the fact that *Anuraeas* are often sucked out by other rotifers and the empty shells deposited at the bottom of the vessels. The proportions of the body with which a rotifer is born are as far as we know and apart from a few exceptions almost the same during the whole of its life; if any parts of the body increase excessively during growth it is improbable that this is connected with the great yearly variations in the external medium. —

If now I combine the three above-named facts: that we find two kinds of females among the Rotifera, that care of the young only very rarely takes place, and that moults are wanting, it seems evident to me that there is a much slighter possibility that the great yearly variations in the external medium should create regular seasonal variations in the rotifers than in the Cladocera, where we have only one kind of female, where we find care of the young, and where the specimens are subject to a series of moults.

The main point is that among the Cladocera as well as the Rotifera we never find conspicuous seasonal variations in the bottom forms, but only in the free-swimming ones adapted to life in the central parts of lakes and ponds where supporting planes are wanting, and the bearing power of the freshwater is subject to regular yearly variations. Furthermore, seasonal variations in both groups are only present in the perennial forms, not in forms which only appear a few months of the year (*Leptodora*, *Bythotrephes*, *Daphnella*, *Ploesoma Hudsoni*, *Gastropus stylifer*, *Rattulus cylindricus* and other pronounced summer forms). Nothing shows in a more conspicuous way the correctness of the buoyancy theory, than the fact that the different components of the freshwater plancton, belonging to widely separated groups of the animal and vegetable kingdom, show seasonal variations. That these variations in the different groups manifest themselves in a different way according to their different construction is to me a matter of course and comes in the second line. In two very valuable papers LUNTZ (1928 p. 451, 1929 p. 465) has tried to ascer-



tain experimentally, whether variation in temperature could produce form variations (the medium was *Brachionus Bakeri* forma *rheanus*). This was not the case and could not in my opinion be expected. To me it is a question whether the form variations which *B. Bakeri* shows in nature have anything to do with seasonal variations. On the other hand, it was of the greatest interest that LUNTZ could show experimentally that, by means of variations in specific gravity, *Brachionus Bakeri* was able to respond to variations in the falling velocity dependent upon variations in temperature. In the last paper (1929) LUNTZ has shown that of specimens of *Brachionus Bakeri* var. *rheanus* caught in May and July the summer form *typica* possessed a falling velocity which was 20 % lower than that of the spring form var. *rheanus*. It was furthermore shown that species without seasonal variation (*Euchlanis triquetra*) in July had a falling velocity which was 30 % lower than in May. The specific gravity of *Brachionus bakeri* was the same for the main form and the *forma rheanus*, in other words the variations in the falling velocity must be referred to variations in body form. In *Euchlanis* the body form was unaltered, and here it could be shown that the specific gravity was altered from 1.027 in the spring to 1.02 in the summer. The first responded to the claims for greater buoyancy by means of form variation, the second by means of variations in specific gravity. Finally LUNTZ arrives at the entirely correct view that the dispute relating to the ecological significance of the body variations is of small significance, because buoyancy organs may also act as "Steuerorgane", and these as well as organs of stability also as buoyancy organs; in 1926 (p. 174) I arrived at quite the same result. The crista of the *Hyalodaphnias*, the peculiar structures of the *Bosmina* may be regarded as buoyancy organs as well as means by which the swimming motion is horizontalized. For it must be remembered that organs which serve to hold the organisms above the thermocline may also act as structures which govern the rate of falling i. e. act as buoyancy organs. The theory of the organs as "Steuer" and "Stabilisierungsorgane" is based on the buoyancy theory; in this way the latter is deepened, but it is by no means made superfluous, without it the former is left suspended in mid-air. As often mentioned before, most of the seasonal variations have been regarded by some of the authors as adaptations on the part of the organisms to the great yearly recurring regular variations in all those external factors which vary in accordance with variation in temperature; because these seasonal variations in reality were very often at variance with the buoyancy theory, they were used by others as weapons against it.

The now published investigation, which has been carried on for years in the same ponds especially with *Anuraea*, have, however, furthermore shown that the occurrence of many of these seasonal variations is dependent on the distance of the generation from a sexual period and the resting-egg. The outdoor observations have here corroborated the laboratory work of KRÄTSCHMAR (1908). Everywhere where more thorough investigations have been carried out it has been shown (*Anuraea aculeata*, *cochlearis*, *Asplanchna priodonta*, *A. Sieboldi*, *Brachionus pala*) that

the form directly derived from the resting egg is the typical one; it is furthermore characterized by its great size and long spines in the *Anuraea* species and no spines in the *Brachionus pala*. The further the generations are removed from the resting egg, the more many of them diminish in size. This process is not, as has hitherto been supposed, limited to a single year but may be continued over several years. For it would seem that several species propagate parthenogenetically in many localities, without any sexual periods for more than one year. —

It would further seem that the many peculiar forms in the genera *Anuraea* and *Brachionus* which were formerly regarded as species, are often of remarkably small size and furthermore mainly occur before a sexual period. It is as if they must in some way be regarded as degenerate, and that the sexual period has the significance of a process of renovation. They are not limited either to the last generation of amictic females or to the mictic ones, but belong equally to both; commonly they occur in the latter period of a great maximum and very often disappear after it and the sexual period. It is as if the want of amphimixis augments the possibility of variations caused by a combination of external and internal factors (varying from year to year and from locality to locality, but acting with a certain regularity), so causing the appearance in a given locality of ever recurring forms, which are all in spite of small aberrations connected with the main form derived from the resting-egg. Then when amphimixis sets in during the sexual period, all these aberrations are eliminated, and the colony reverts to its normal specific aspect.

In some cases it seems as if colonies in certain localities so to speak become fixed for years or perhaps for ever in one of these stages of the developmental series. This may be the case e. g. with *A. valga* and *A. tecta*. Localities are known where all *A. aculeata* year after year only occur as *A. valga* and others where all *A. cochlearis* occur as *A. tecta*, and there are other localities where the two forms *A. cochlearis* and *A. tecta*, at all events for years, live side by side. It seems as if links in the developmental chain have a specific range here; this may be true, but the salient point, that these forms *A. tecta*, *A. valga* are hatched from resting-eggs, is still a desideratum. On the other hand in some localities, and especially in the pelagic region of larger lakes, it seems that the main form derived from the resting egg, e. g. *A. cochlearis* forma *robusta*, may be the main form for years, without showing any sign of degeneration.

In numerous cases the two cycles, the cycle of external conditions i. e. the yearly regularly recurring variations in temperature, specific gravity and viscosity and the internal one, causing diminution in size, irregularities or diminution of thorns, maxima, sexual periods, formation of resting eggs, minima and when the resting eggs are hatched, robust forms with long thorns, coincide; on the other hand, in very many cases such a connection cannot be shown. It is obvious that we have here a very rich material which may be used as a support for as well as against the buoyancy theory. In reality many of these form variations of the Rotifera have

most probably very little to do with the yearly variations in the bearing power of the freshwater.

On the other hand, I am fully convinced that several structural peculiarities, suddenly appearing in some of the colonies of the species, may be regarded as adaptations to the variations in the bearing power of freshwater. These variations always occur at the highest temperatures, by no means in all localities, on the contrary, very irregularly temporally as well as locally. I refer here to the peculiar jelly coatings round the carapace of *Brachionus angularis*, the coatings of asperities on the carapace of *A. cochlearis*, and perhaps the irregularity in the facets of the carapace of *cochlearis* and *aculeata*, furthermore a remarkable thickness of the anterior and posterior thorns and often highly pronounced outward curvature of the posterior thorns, causing them to diverge strongly. Most of these characters may help in different ways to retard the falling motion, and so may well be regarded as adaptations to a diminution in the bearing power of freshwater at the highest temperature; as far as I know, they are all absent in specimens belonging to the winter months. In this connection I may also make reference to the observation that the long posterior thorns of *B. amphicerus* during swimming are stretched backwards, but when the wheel-organ is withdrawn held vertically to the longitudinal axis of the body; we find quite the same motion with regard to the thorns of *Triarthra breviseta*, *longiseta* and the arms of *Pedalion*.

### Some biological Remarks.

As mentioned elsewhere (DE BEAUCHAMP, W-L.), the rotifers are regarded as originally creeping organisms belonging to the bottom of the littoral zone with its stones, its mud and its vegetation. From this they have emancipated themselves and to a smaller or greater extent become changed into free-swimming slowly rotating organisms. Most of the forms have their home among the vegetation, living a half creeping half swimming life between leaves and stems. A rather small number have emancipated themselves from a substratum of any kind, living a true pelagic life in the central vegetation-free part of our ponds or even in the pelagic region of the largest lakes. —

The number of these forms is not very high; it can only with difficulty be brought up to 100 species only  $\frac{1}{15}$  of all known rotifer species. Regarding the *Notommatidae* as the most primitive forms, it seems as if lines ending in the most pronounced planctonic species have developed from rather different offspring in the *Notommatidae* and allied families. It must, however, be kept in mind that however much the type is altered, it always returns as a resting egg to its native home, and that most of the rotifers really pass the longest time there as resting eggs, furthermore that the pelagic characters as a rule are least developed in the generation hatched from the resting-eggs. This generation is the most primitive one and has most of the ancestral stamp. It may be shown that the more the type

emancipates itself from any substratum, the more the organism is morphologically and biologically altered. As far as I have been able to see, these alterations occur especially in four different directions, viz.

1. the manner in which the organisms get their food.
2. the deposition of the eggs.
3. the transformation and reduction of the male sex; with regard to this point see Part I, 1923.
4. the seasonal variations; see above.

1. I shall not here enter into the manner in which the mouth parts and the wheel organ are altered in accordance with the claims the life conditions impose upon organisms which were originally bottom forms, but which are to be adapted to get their food in the waterlayers. I make reference here to Handbuch der Zoologie (Rotifera) 1929, Vol. II. A good deal, especially the *Brachionus* and *Anuræa* species, the pelagic *Melicertidæ*, *Floscularidæ*, *Pedalionidæ* and *Pompholyx* are nannoplankton-or detritus feeders, which catch the nannoplankton during swimming; the plankton is caught by the wheel-organ, and carried to the mouth by means of special bristles or wreaths of cilia. Others are true animals of prey, but they treat the prey in a very different manner: some of them, the *Asplanchnadæ*, seize the prey either by means of the mouth parts which are carried as claspers into or in front of the mouth opening; this may also be the case with the *Synchaetadæ*, even if here a sort of sucking action is present, too. This manner of procuring food requires a large reservoir, in which the whole organism caught by the mouthparts can be magazined and chemically prepared before it reaches the real digesting part of the alimentary canal. We therefore often see a large gizzard-like part before the oesophagus distended with *Anuræas*, *Peridinium* and *Triarthra* whose long bristles protrude through the mouth opening. The decomposing state in which the prey is, shows that it is under chemical influence. The stomach itself is small.

Many of the plankton organisms treat the prey in quite another way. It is seized by means of the mouth parts; parts of the coronal disc lying round the mouth opening, combined with folds belonging to the mouth parts, are pressed against the victim, which is held fast by a sucking action; then the mouth parts, acting like a piston, begin to bore a hole in the skin or carapace. This done, the contents of the victim are pumped into the alimentary canal. The prey is very often *Peridinium*, *Ceratium*, now and then also other Rotifers e. g. *Anuræa*, *Triarthra*. In its most elaborated form this type seems able to pursue definite prey, swimming a few millim. before it. I have seen the *Ploesoma Hudsoni* in this way pursuing *Peridinium* and *Anuræa*; most probably the pursuit is not possible with a rotating motion; it is very interesting to see how the motion during the pursuit changes into the straight one.

Rotifers of this type possess, on the coronal disc, well-developed palpar organs, sensitive hairs, and remarkably highly developed eyespots, further a well developed dorsal organ. —

The whole mastax is very elongate, and extremely mobile, especially in the pelagic *Rattulidae*, and the oesophagus is commonly not inserted at the bottom of the mastax, but high up on the dorsal side. The stomach is commonly an enormous sack, filling, with its many diverticules, almost the whole interior of the animal; the gastral glands are not always well developed and show signs of degeneration; in the same species they are subject to great variation with regard to size as well as form. Many of these forms seem to possess an intracellular digestion; the cells contain enormous amounts of small irregular pieces which more closely studied manifest themselves as parcels of chromatophores. An anus may perhaps be present but is most probably not used after the first days of life. The cells and later on the stomach contains large irregular black balls; in some of the rotifers the stomach cavity seems only to be a reservoir for digested material which is preserved in the empty carapace after the death of the animal (*Ascomorpha*). In some cases it seems doubtful if the stomach cells carry cilia. In the interior of the stomach whole organisms are never found, only a pulpy mass, very often of a green colour, which, when more thoroughly studied, in many cases manifests itself as chromatophores belonging to the sucked out prey. During decomposition these chromatophores change from a green to a yellow, brown, and at last to a black colour. Hence many of these organisms belong to the most highly coloured rotifers we know. This holds good especially of *Gastropus styliifer*, *Gastropus minor*, *Sacculus viridis*, which, as far as I know, belong to the same biological groups, *Anapus testudo*, *ovalis* and *Ascomorpha agilis*. —

2. As is well known, the rotifers belonging to the bottom and the vegetation deposit their eggs upon a substratum; very often they are simply dropped off upon it; often they are agglutinated singly or in small batches (*Euchlanis*). Very often a number of females select a spot in which they simultaneously or at very short intervals agglutinate the eggs. This results in eggspots of several hundred eggs now and then consisting of all three sorts of eggs; the males hatched from the male eggs encircle the eggspots and pair with the females (*Hydatina*). It is a matter of course that all those rotifers which belong to the pelagic region, where substrata fail to occur, are forced to solve the question with regard to the placing of the eggs in another manner. Now it is very interesting to see, in how many different ways the problem is solved; this very fact, that almost every one of the pelagic Rotifera has adopted a special way, shows that here really is a difficulty to overcome, an environmental demand, solved in accordance with the specific structure of the said rotifer type. The whole question is complicated by the fact that the different kinds of eggs in the very same species are deposited in quite a different manner. —

The most primitive mode is simply to drop the eggs into the water. This for instance unquestionably often takes place with the resting-eggs of the *Asplanchna*

and of the *Synchaeta*, *Rattulidae*, *Anuraeadae*, *Anapus*, *Pedalion*; in some cases observations seem to show that the resting eggs are not dropped, but stay in the mother-animal and then subside together with its empty carapace. This is e. g. most probably the case with the *Triarthra* species, *Rhinops vitrea* and others. A common feature in all these resting-eggs is in the first place the peculiar and often very complicated structure of the egg-shell; commonly the shells are provided with short spines (the resting-eggs of *Synchaeta*, *Polyarthra*, *Anuraea aculeata*, *cochlearis*, *Rhinops* a. o.) a structure which these resting-eggs very often share with those of rotifers living in the benthos. Curiously enough, these structures often vary from habitat to habitat among the same species, often in such a way that in one locality the shell has spines in the other none (*Anuraea*, *Brachionus*). In other cases the shell structure has a squamose aspect, as is the case with most of the *Asplanchna* species; this may be further developed by *Triarthra* where the egg is surrounded by a mantle of large spaces, which invariably reminds one of the air spaces round the statoblasts of Bryozoa and the ephippia of certain Cladocera. In other cases the egg, surrounded by a very thin inner shell, lies in a real egg capsulè, much larger than the egg itself. This is the case with *Brachionus*-eggs.

According to these structures one would expect to find these eggs on the surface of the water and not at the bottom. The strange thing is that, as long as they are carried by the mother animals, the eggs contain no air-globules; the eggs disappear after the large maxima and most probably sink to the bottom. In early spring we find the surface in the bays of our lakes and lake ponds covered with countless numbers of ephippia and small brown eggs, in fact, the *Brachionus*-eggs; these eggs contain a great air bubble, which fills out the space between egg-shell and egg; later on, when the embryo has grown larger, the bubble is forced backward in the shell, and it may be shown how the young one works with the wheel-organ in the inner egg-shell in near contact with the air bubble. The egg is provided with a furrow, delimiting a hood, which bursts during the liberation of the embryo. Later on the empty eggs are found still containing the air bubble, and the remnants of a hyaline membrane, the inner egg-shell. The air bubble can only be produced by the embryo itself, during the development. These observations already mentioned in 1909 (p. 432), would lead to the supposition that eggs with a similar structure of the shell, in the first place of *Triarthra*, *A. Brightwelli* and allied species, furthermore *Conochiloides natans*, would behave in a similar manner. Curiously enough, I have, however, never been able to find these eggs on the surface of our waters. On the other hand, in early spring, I have found these resting eggs to be pelagic, before the great maxima, but only in deeper water-layers. I have been of opinion that production of air raised the eggs from the bottom and that the eggs developed in the midmost water-layers. I am not able to furnish any proof of this supposition. —

As is well known, the pelagic eggs of the sea very often contain large oil globules, intended to keep the eggs floating. Oil globules are not or only faintly

developed in the eggs of bottom rotifers; on the other hand, they are by no means rare in the eggs of pelagic species. They are found in the female parthenogenetic eggs of *Polyarthra* which carries its eggs, in the eggs of *Synchaeta* and in the resting-eggs of *Asplanchna priodonta*. Some of the *Synchaeta* species seem, at all events in some localities, to carry their eggs, commonly they are dropped in the water; this is the rule with the eggs of *S. pectinata*. If we remember that the summer eggs may be hatched in the course of only a few hours, and at all events at higher temperatures, in the course of half a day, it may be doubtful whether these eggs, even if they are deposited upon the bottom in our vessels, are not able, in water columns of only a few metres, to keep afloat till they are hatched. What happens in the case of the resting-eggs of *A. priodonta* I do not know. Even in ponds coloured milky by the species I have never seen the eggs, never found them on the surface nor in the midmost water-layers. —

Some species have adapted themselves to the environment in another manner. Their summer eggs are surrounded by a thick layer of jelly in which the egg floats; in addition they are surrounded by a fine, very thin membrane. These eggs are found among *Bipalpus vesiculosus*, they are very common in pelagic samples from many of our smaller ponds and lakes, especially during the summer. — Another floating principle is used by some *Synchaetas*, whose summer eggs are provided with very long bristles. They have been well figured by ROUSSELET (1902) hitherto I have not myself been able to find these eggs.

Another way of overcoming the difficulties is that the rotifers themselves carry the eggs till the time of hatching, attached to the posterior part of the body. This is the case with the summer eggs among *Polyarthra*, *Pompholyx*, *Pedalion*, all the *Anuræa*- and *Brachionus* species and *Triarthra*. Whereas the other above-named species carry the resting eggs till they are dropped off or the female is dead, *Triarthra* only carries the summer eggs attached to the posterior part of the body, the resting-egg being carried within the body. The material which is used to agglutinate the eggs to the body is most probably a gelatinous matter deriving from the foot glands, which are often preserved even if the foot, as is the case with many plancton organisms, is either totally lost or reduced; the genus *Pompholyx* carry the eggs on long thin stalks, which can partly be drawn into the body and again protruded. — Some plancton rotifers develop all their eggs in the body; with regard to the summer eggs the oviduct is used as a form of uterus in which the eggs are developed. This is the case with *Asplanchna*, *Rhinops* and *Conochilus*; these forms are viviparous or ovoviparous with regard to the parthenogenetic female eggs and male eggs. Besides it must be remembered that viviparity is also found among bottom forms, especially *Rotifer* and *Apsilus*.

A very peculiar way of solving the question of placing the eggs is employed by those rotifers which attach their eggs to other plancton organisms; in this way they have found even in the pelagic region, a substratum to which the eggs may be attached. This is in the first place the case with some *Rattulidæ* which mainly

throw their summer eggs on *Brachionus* species especially *B. angularis*; furthermore with *Ascomorpha agilis*, mainly using *Uroglena volvox* as a substratum for the summer eggs; *Bipalpus vesiculosus*, which most probably uses *Melosina* threads for the resting-egg, furthermore *Rattulus stylifer*, using *Dinobryum*. Apart from *B. vesiculosus*, all the species drop the resting-eggs into the water. —

The pelagic *Floscularidae* carry all their three kinds of eggs in the gelatinous sheaths.

### Concluding Remarks.

1. In the first part of this work (1923) the males of the Rotifera were treated; in addition I tried to give an explanation of the reduction of the male sex of the Rotifera. On the basis of studies carried out for more than 30 years I have now tried to give some contributions to the periodicity and sexual biology of the Rotifera. During these years many hundred drawings have been made. On the accompanying 15 plates some of them have been published; they illustrate only what I have been able to see in the living animals.

2. As an aid in the attempt to understand the biology and especially the sexual biology of the Rotifera I have considered it necessary first to give a rather extensive account of the results hitherto gained with regard to the sexual biology and a more abbreviated one with regard to the cyclomorphoses.

3. A short sketch of the nature of my area of exploration has been given. It has been shown (p. 45) how one of the explored ponds, Funke Pond, has altered during the period 1880—1930 and how the desiccation has influenced the fauna, especially its plancton.

4. A comparison between the Danish lake and pond-plancton has been given; this comparison is based on a great number of single observations, made in about 30 years; the results are only given in broad features. In the first place it has been pointed out that, whereas the composition of the plancton in our lakes is almost the same everywhere, the pond plancton during the summer months shows, locally and temporally, the greatest possible variation; during the winter months this variation is by no means so large. The differences in seasonal variations in lakes and ponds have been mentioned. —

5. With regard to the chemical and thermal conditions of our freshwaters stress has especially been laid upon the temperature, quite especially upon the elucidation of the duration of the freezing periods. It has been shown that these periods, with regard to duration as well behaviour in different directions, vary extremely from year to year and also in the same year but in different localities. Our different freshwaters show great differences. Means have been mentioned which contribute something to the understanding of these differences.

Also the high temperatures in early spring on sunny days upon the sheltered sides of ice-bound ponds and lakes, with a southern exposure a few inches from the ice, and furthermore the extremely high temperature in sheltered small creeks



and coves at the highest summer temperatures have been mentioned. It has been shown how these temperatures must necessarily influence all the organic life of our freshwaters and examples of that influence have been given.

6. The pH values of a good many ponds, and especially of those which have been most thoroughly studied, have been given. As is well known, HARRING and MYERS, with regard to the local distribution, and TAUSON, with regard to the biology of the single species of the Rotifera, have tried to find in the pH values the main factor which governs the geographical distribution and also the life of the organisms. The investigations seem to show that this factor has been somewhat overrated; the tables on pp. 71—74 show that 10 rotifer species are regular inhabitants of our most alkaline freshwaters with pH 8.4 as well as of ponds with pH only 4.8.

7. The investigation has been unable to elucidate anything with regard to the propagation of the *Bdelloida*.

When it has been impossible, in the laboratory, to produce sexual periods and males in some of the *Notommatida*, it may be pointed out that it is just in this family that great maxima have been observed during the outdoor investigations, though they were not followed by sexual periods; males have either never been seen, or only in very limited number; it would seem that propagation among some of the rotifers, apart from the *Bdelloida*, is mainly parthenogenetic in our latitudes, males are not present every year and their number may be much smaller than that of the females.

8. The very interesting point in the propagation of the Rotifera, that, apart from the *Bdelloida* and perhaps some *Notommatida*, they possess two kinds of females, amictic and mictic ones, is corroborated by outdoor investigations wherever such investigations were able to do so. It is a matter of course that such investigations cannot contribute to the solution of the question in all those cases where the females throw their eggs or agglutinate them to a substratum. On the other hand, in all those cases where the females carry their eggs, it will easily be understood that if we could find females which simultaneously carried either parthenogenetic female eggs and male eggs or parthenogenetic eggs and resting-eggs, the pointing out of two female forms would be wrong. Now the numerous investigations in nature show that we do not know a single case where a female has carried an amictic egg together with a male or resting egg. Either we find females with parthenogenetic female eggs, or females with one of the other kinds of egg, or females which carry these two either simultaneously or successively. The last fact only means that the mictic female has been fecundated after the beginning of the period of egg-laying.

From a biological and perhaps also from a phylogenetic point of view the amictic female is comparable with the sporocyst of the Trematoda; its main task is greatly to augment the number of individuals deriving from one single egg-cell. As a free-swimming organism and belonging to a group of animals where hermaphro-

ditism does not exist, it is not subject to all those modifications which parasitism and hermaphroditism involve.

9. All outdoor investigations corroborate the fact that females hatched from resting eggs are always amictic. Even in colonies with the shortest active life e. g. *Rhinops*, *A. Sieboldi*, the first observed specimens are always amictic females, males and females carrying resting-eggs or male young ones always appear at a later date.

Under normal life conditions the appearance of mictic females is limited to the second or third generation after the resting-egg, at all events among organisms bound to drying ponds as long as they live under life conditions characteristic of these ponds. Most colonies are, in the middle of their lifetime, in a labile period in which external conditions may influence propagation. This period intervenes between periods in which this is not the case. During the first period the propagation is amictic, during the last mainly mictic. —

10. Investigations of the kind now published cannot of course indicate the nature of those variations in external conditions which seem to cause the appearance and disappearance of mictic females. As far as I can see, variations in the chemical composition of the freshwater seem to be the most important here. In some cases it has been shown that variations in nourishment seem to be of secondary importance (*Asplanchna* Torokeri pond). It seems as if the power of external conditions to bring a sexual period to a stand still is greater than their power to initiate one. Hereditary characters gained by accumulative powers have stamped the organisms with regard to this last named point.

There is no doubt that the regularly recurring yearly variations in the life conditions in a certain locality have in numerous colonies caused fixation of the time for the appearance of the sexual periods, a fixation which so to speak stands on the threshold of hereditary characters or has even overstepped it.

That abnormal laboratory conditions may be able to alter this fixation is another matter and from a point of view, regarding the normal biology of the animals, only to be regarded as pathological and comparable with pathological monstrosities originating in and cultivated under laboratory conditions.

The observations of WHITNEY and SHULL that lines obtained from widely separated localities yield a constantly differing proportion of mictic females and behave in a very different manner with regard to the number of eggs are corroborated in numerous cases; they may perhaps be extended as follows: every line has its own form for propagation, developed through the accumulation of small annual adaptations to the environment. Every line has a distinct tendency to propagate in a distinct manner; this manner is not equally well fixed in all lines; variations in external conditions may influence the inherited dispositions in very different degrees.

11. The life history of *Hydatina senta* under natural life conditions has been studied upon a regular series of observations in nature. It has been shown that

the period of active life does not last more than 4—6 weeks. The rest of the year is passed in a latent stage as resting-eggs. The natural home of the animal is ponds polluted by manure. This last named result is in accordance with those gained through the studies in the laboratory.

A colony of *Asplanchna Sieboldi* has been studied in a little pond near Hillerød and the results combined with studies in the laboratory.

These studies of *Hydatina* and *Asplanchna* have revealed a series of facts relating to the duration of life of the amictic and mictic females and the males during the different periods; further facts relating to fecundity, propagation and the number of resting-eggs. The way in which a line turns from amictic to mictic propagation is shown. With regard to all these points I refer the reader especially to pag. 106 and pag. 153. The following points may especially be emphasized.

12. When several authors (MAUPAS, PUNNETT, WHITNEY and MITCHELL) have maintained that fecundation is only of importance if it takes place in the first hours of the life of the young females, combined out- and indoor investigations have shown that, as stated by several other authors, this assertion has no general validity. When females of *A. Sieboldi*, as stated above, begin with the propagation of males and then form resting-eggs, this can only be understood to mean that the female has been fecundated at a later time of its life.

13. The observation that species in aquaria appear and disappear at quite regular intervals is in full accordance with the investigations carried on in nature. It is of interest that the periodicity of the Rotifera is also observed in aquaria. —

14. With regard to *A. priodonta* in its typical form it has been supposed that the lifetime of the single individual during winter at temperatures near zero is much longer than during summer.

15. The observation made in the laboratory that mictic females appear at the height of the development, is only a corroboration of the old fact often observed during the investigations in nature, that a great maximum almost always develops before the appearance of the males. It must merely be added that in nature very often great maxima are developed without any development of males. In many cases this phenomenon coincides with sudden and great variations in meteorological conditions, in the first place in temperature and rainfall, causing e. g. a sudden and enormous dilution of the water. It may, however, happen that the maximum is brought to an end without any visible variation in the external medium. If then material from such maxima is taken into vessels, the animals invariably die out whether they are kept together or isolated, even if natural food is present in abundance (*Triphylus*, *Gastropus minor*). This would seem to suggest that there really, as PUNNETT has conjectured, may be lines in which a sexual period has dropped out and only rarely and under exceptional conditions, not under those afforded by the normal environment, will appear again. There is very little doubt left that these lines, identical with those which outdoor naturalists have designated as acyclic, really exist in the pelagic region of larger lakes, where they may be

identified with the well-known and often studied acyclic races of plancton cladocera.

It seems, furthermore, that apart from the *Bdelloida* many *Notommatidae* and also some species belonging to the Fam. *Cathypnadae* (*Lecane*) belong to the same category. —

16. The investigations have not revealed a single example of external differences between mictic and amictic females in their active stage; in the egg stage there may be great differences. Only with regard to size there may be a slight difference; this applies especially to some *Asplanchna* colonies where the amictic spring females are much larger than the mictic generations born later on. Even if the lines offer examples of the greatest variability (*Asplanchna Sieboldi*, *Anuraea cochlearis*, *A. aculeata*) all the forms may propagate as well amictically as mictically.

Nevertheless, physiologically and biologically, the two kinds of females differ from each other. Even if for the present we are not able to show it, they must also do so anatomically.

It must be kept in mind that in the egg-stage there is usually the greatest difference between the eggs worked out by an amictic and by a mictic mother; this applies especially to the resting-egg. As it is only the mictic female which is able to produce resting-eggs, and which stores great amounts of fat and oil in its vitellarium and uses the stored material for production of one or a few eggs, we are entitled to assume that the two females may differ very much in their metabolic processes. Furthermore the mictic female in contrast to the amictic one, is able to subdivide the amount of yolk mass into very small amounts and, as is the case with *Triarthra Polygarthra*, *Pedalion*, suddenly produce simultaneously about 12 eggs (male eggs) whereas the amictic females produce the eggs successively.

Furthermore, as we know that the shells of the resting-eggs in very many cases are equipped with thorns, jelly structures, air-chambers, characteristic of the single specimens, whereas the shells of the eggs laid by amictic mothers are always smooth, we are almost forced to believe that the genital organs of the mictic females are provided with glandular cells, which are not present in the amictic ones. That differences in the sexual organs may be present, especially in those cases where the amictic female is viviparous, and the mictic female if fecundated, oviparous, seems evident. In this connection we may perhaps call attention to the following fact. If an amictic female is viviparous, the mictic female is so, too, with regard to the male sex, and if the amictic female is oviparous, the mictic female is so, too. We do not know any case where the production of males is not in accordance with the production of amictic progeny. —

There may also be great differences in the behaviour of the two kinds of females; the amictic female may drop its pelagic egg in the watermasses but the mictic one agglutinates the resting-egg to *Melosira* threads. In contradistinction to this the amictic mothers of *Ascomorpha agilis* and some *Rattulidae* agglutinate their eggs to other plancton organisms, whereas the mictic mothers drop the resting-eggs

to the bottom. In some rotifers the amictic mothers carry their eggs, whereas the mictic ones most probably die with the resting-eggs in their body, these being only liberated upon the decomposition of the mother's body (most probably *Triarthra*).

It may furthermore be pointed out that among many plancton organisms the amictic females are pronounced positively heliotropic animals, whereas the mictic ones are negatively heliotropic, gathering at the sides of the vessels opposite to the light. This at all events is the case when they carry resting-eggs. It may further be added that it may be possible that amictic and mictic females may live quite a different life; this may be the case with the rotifers parasitic in *Vaucheria* and *Volvox* where the mictic ones are most probably parasitic all their lives, whereas the amictic ones may have a free stage.

17. With regard to periodicity the species investigated have been referred to 5 types: 1. the type of drying pools (*Hydatina* type), 2. the rotifers living in small permanent ponds and with the active life terminating in a sexual period in the early spring (type: *Rhinops*), 3. the rotifers living in permanent ponds or lakes and where amictic females are often present after the sexual period (type: *Asplanchna* species o. a.) filling out the gap either between two sexual periods during summer or between the autumnal sexual period and the hatching of the hibernating resting-eggs (*Anuræa* type) (poly- di- monocyclic, acyclic, colonies according to habitat). 4. Summer forms hatched in June and disappearing in September (*Gastropus stylifer* type). Winter forms appearing in Nov., Dec. and disappearing in May (*Notholca* type). 5. Acyclic forms. A sharp distinction between polocyclic, dicyclic and acyclic forms has no scientific value. —

18. The investigations relating to the *Anuræa*, the *Brachionus* and the *Asplanchna* seem to show that the course of the seasonal variations differs from colony to colony, and that this course is fixed in form as long as the colony lives under the same life conditions. Hatched from resting-eggs all colonies have almost the same appearance but during the development they grow less and less alike, and each colony develops its own characters (the different *Brachionus* races: some with thorns, some with short thorns, some with very long thorns, the development of the races of *A. priodonta*, in ponds, in Hald lake).

It seems as if colonies do not deviate uniformly every year (*A. Brightwelli*; *A. Sieboldi*).

Also with regard to the temperature at which the resting-eggs are hatched the colonies differ very much from each other (*B. pala*, *A. Sieboldi*, *A. Brightwelli*) and it seems as if those hatched at the highest summer temperatures are most inclined to differ from the normal aspect of the species.

The investigations relating to the *Anuræa* and especially to *A. aculeata*, seem to show that it may take more than one year before the whole developmental series of seasonal variations from long-thorned to thornless forms has been run through.

19. The seasonal variations of the *Anuræa* (*A. aculeata* and *cochlearis*), the difference in the length of spines, diminution in size etc. which very often occur

immediately before a sexual period combined with the fact that the forms derived from resting-eggs are the largest and have the best developed spines, seem to corroborate the view that parthenogenetic propagation carried on for a long time may weaken the colonies; furthermore that the unfortunate consequences may be neutralized by mictic propagation.

20. The seasonal variations of the Rotifera can only in slight degree be identified with those of the Cladocera. Since we find two kinds of females among the Rotifera, and care of the young ones only very rarely takes place and moults are wanting, it seems evident that the great yearly variations in the external medium have much slighter capacities for creating regular seasonal variations in Rotifera than in Cladocera, where we have only one sort of female, care of young ones and moults. Many of the seasonal variations, especially those of *Anuraea*, are dependent upon the distance of the generation from a sexual period and the resting-egg; they express a degeneration; they are governed by an internal cycle and compensated by amphimixis. As seasonal variations dependent upon variations in the external medium may be regarded: the jelly coating round the carapace of *B. angularis*, the coatings of asperities on the carapace of *A. cochlearis*, the thickness and curvatures of the thorns, the seasonal variations of *Asplanchna* and some *B. pala* series. —

21. Colonies may be found which seem genotypically stamped in their seasonal variation either in the way that the species year after year is only represented in the last stage of the developmental series (*Anuraea tecta*; *A. valga*), or in the way that their seasonal variations show peculiarities only very rarely found otherwise (*Brachionus pala* Fjenneslev Pond; *Asplanchna priodonta* Hald Lake).

22. With regard to the position of the Rotifera in relation to the buoyancy theory stress may be laid upon the following point. The more the Rotifera pass from benthonic to pelagic life, the more they become perennial plancton organisms, the greater is their variability, locally as well as temporally. Just this result would be required by the buoyancy theory if it were right. On the other hand it is not to be expected that the regular annual variations in the external medium shall manifest themselves in quite the same manner in two sections of the animal kingdom differing so much from each other as the Crustacea and Vermes really do.

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With the publication of the second part of this work I have finished a task which has occupied me very much during the last thirty years. I am fully convinced that several points would have been better elucidated if the publication had been deferred another few years. Nevertheless owing to other investigations, carried on simultaneously, I find it most convenient to publish already now.

In several particulars it differs a good deal from the modern literature relating to the biology of the Rotifera. During the last thirty years, especially in the years after the war, it has become the custom with regard to the Rotifera as well as a very great deal of all limnological literature and I am tempted to say, as far

as my experience goes, with a great deal of scientific literature in general, to publish the observations in long series of very short papers most of them of only a few pages. The figures accompanying these papers can only rarely compare in exactness and hardly ever in beauty with the plates accompanying the papers from an earlier period.

All these small papers are scattered over an enormous number of often very small periodicals. There is no denying that this mode of procedure may be very convenient to the authors, on the other hand, it undoubtedly throws great difficulties in the way of their successors. It seems as if the want of stability and the restless hurry so characteristic of our time has set its mark on a good deal of scientific work. After this had been written it was with the greatest interest that I saw that METCALF has set forth quite the same thoughts in 1929 (p. 269); he says as follows: "We discourage the publication of comprehensive studies adequately illustrated and use our facilities for publication mostly for a short paper with a minimum of pictorial illustration." And further, on p. 270: "Our present tendency towards hasty publication is, to be sure, in line with the jazz spirit in art, literature and music, indeed in life itself, having at its root unwillingness to do prolonged and faithful work before seeking expression and advertisement." —

Since LAUTERBORN's investigations most of the researches relating to the biology of the Rotifera, especially the sexual biology, have been carried out in the laboratory, my own as far as possible in nature. As far as I can see, experience shows that in nature it is much more difficult to get a definite answer to our questions than in the laboratories. On studying the biology of the animals in nature we learn at a very early stage of the investigations that the organisms are only able in a normal manner to react in the way desired in quite definite and often very short periods of their life; apart from these periods the organisms are either unable to react, or their reactions will only express pathological states and are therefore not to be regarded as normal. It will further be evident that the organisms can answer the questions we wish to solve in very different ways and that in the struggle for existence they have more than one string to their bow. — Furthermore that different colonies of the same species but living under quite different conditions will by no means answer the questions put to them in the same way. If this is correct, we shall arrive at the following results with regard to laboratory investigations.

If two laboratory investigators in quite different parts of the globe, at a moment only convenient to them, go out to the nearest possible locality and at haphazard take a colony of the same species into the laboratory for experimental purposes, they will almost always get quite different answers; and that even if they expose them to the same external conditions and try to elucidate the same problem. Very often they will run the risk that the answers only express pathological states. The answers which can be gained in the laboratory in a relatively short time only rarely lack sharpness especially in those cases where the organisms die. On the other hand in very many cases they do not express normal condi-

tions. Furthermore as the laboratory investigations can unquestionably be planned according to much more exact methods than those in nature, it is no wonder that the results, though as a rule very contradictory, are commonly published in a form which dazzles the reader by its conciseness and leaves no doubt as to the blind confidence to the author in the value of his results.

This may go so far that laboratory investigators maintain that opinions arrived at as a result of a number of regular investigations year after year in the same locality and where the phenomena are studied with the utmost care are mentioned as only "theoretisch", and only what is carried on in the laboratory gets the predicate "eigene Beobachtungen". — Investigations planned and carried out in nature always take a very long time. The scientific value of the solutions of the problems depends partly upon preliminary studies of the life of the organisms in the selected locality, partly upon the total amount of material of colonies of the same organism but from different localities, collected for comparison. The methods can never attain to the accuracy of those used in laboratory research, and they never tempt the writer to give them a form which dazzles the reader by its exactness. Nevertheless I for my part am tempted to believe that the results gained from studies in nature, even if published in a vaguer form than those of the laboratory, in very many cases have a more general value and therefore, in reality, are nearer to the truth. —

Characteristic of a great deal of the literature relating to the biology of the organisms kept in laboratories is further the ever recurring question whether the variations are caused by external or internal factors. To my mind not a single vital process either normal or abnormal can be referred solely to either internal or external conditions. To me it is upon the web twined of threads of both factors that life depends. —

First of all it shows a want of respect for all hereditary forces combined with an incredible selfconfidence when experimenters suppose that they should be able, with material from a single locality and in that isolated moment of eternity during which an observer casually studies the phenomena, without considering the palæontological evidence, to get a remodelling of inherited fixed characters, and when this remodelling does not take place, especially in this fact see a confirmation of the supposition that acquired characters are not hereditary. —

It has been asserted that the belief that acquired characters can be inherited has become a kind of religion with the Neo-Lamarckians. This may possibly be true. On the other hand, there can, to my mind, be no shadow of a doubt that the blind dogmatic confidence in the results obtained from momentary and locally isolated investigations without due regard to the unlimited areas of space and time through which the organisms live and have lived, is in an even higher degree devoid of that stringency of reasoning and accuracy in experiments upon which the opponents of the Neo-Lamarckians, particularly the modern enquirers into the question of heredity, pride themselves as their chief characteristics.



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## EXPLANATION OF PLATES

All plates reduced one third.

My assistant Mr. Berg has helped me with the "dotting" or shading of the figures, for which help I here tender him my best thanks.

All figures are drawn with Zeis microscope and with camera after living objects; staining and narcotizing methods have not been used.

### Plate I.

Fig. 1. <i>Rhinops vitrea</i> amictic female .....	Obj. 4. Oc. 6
- 2. — male .....	Obj. 4. Oc. 6
- 3. <i>Triarthra longiseta</i> forma <i>mystacina</i> amictic female .....	Obj. 4. Oc. 6
- 4. — — male .....	Obj. 4. Oc. 6

All figures drawn with the same power.

Figs. 1—2 represent a species where the differences in size and structure are but small; figs. 3—4 a species where the difference is extremely large and the male very strongly reduced.

In figure I the numbers designate.

1 Eyes	8 Wheelorgan	14 Vibratile tags	21 Egg
2 Cilia	9 Hypodermal cells of	15 Oesophagus	22 Posterior lateral
3 Ganglia cells	the wheelorgan	16 Gastral glands	organs
4 Nerves	10 Ganglia	17 Stomach	23 Intestine
5 Brain	11 Mouth	18 Excretory canals	24 Contractile vesicle
6 Chitinous lamellæ	12 Mastax	19 Germarium	25 Rectum
7 Auricles	13 Mouth parts	20 Vitellarium	26 Pedal glands

## Plate II.

Fig. 1.	<i>Notommata</i> sp.	strongly pressed; amictic young female	Obj. 4. Oc. 6
- 2.	—	not pressed. The contours normal.	
- 3.	—	seen dorsally; the strong folds in the skin are conspicuous	Obj. 4. Oc. 2
- 4.	—	<i>Daphnia magna</i> with two <i>Notommata</i> sp. and eggs upon the fornices	Obj. 16. "Sucherocular"
- 5.	<i>Notommata</i> sp.		Obj. 4. Oc. 2

## Plate III.

Fig. 1.	<i>Diurella tenuior</i>	amictic female	Obj. 4. Oc. 6
- 2.	—	amictic egg deposited upon <i>Dinobryum</i>	Obj. 4. Oc. 6
- 3.	<i>Diurella stylata</i>	amictic female	Obj. 4. Oc. 6
- 4.	—	posterior part of the body	Obj. 4. Oc. 6
- 5.	—	egg	Obj. 4. Oc. 6
- 6.	—	resting egg	Obj. 4. Oc. 6
- 7.	<i>Rattulus cylindricus</i>	amictic female	Obj. 4. Oc. 4
- 8.	—	Forepart; the wheelorgan withdrawn	Obj. 4. Oc. 4
- 9.	—	amictic egg	Obj. 4. Oc. 4
- 10.	—	male egg	Obj. 4. Oc. 4
- 11.	<i>Rattulus capuzinus</i>	amictic female	Obj. 4. Oc. 6
- 12.	—	forepart of the body strongly protruded	Obj. 4. Oc. 6
- 13.	—	mictic female	Obj. 4. Oc. 4
- 14.	—	amictic female seen from below	Obj. 4. Oc. 4
- 15.	—	forepart seen laterally	Obj. 4. Oc. 6

## Plate IV.

Fig. 1.	<i>Ascomorpha agilis</i>	amictic female. Inanition	hom. Im. Oc. 6
- 2.	—	mictic female, well nourished, seen laterally	Obj. 4. Oc. 6
- 3.	—	carapace	Obj. 4. Oc. 6
- 4.	—	mictic female well nourished, seen from below	Obj. 4. Oc. 4
- 5.	—	mouth parts	hom. Im. Oc. 6
- 6.	—	resting egg	Obj. 4. Oc. 6
- 7.	—	<i>Ascomorpha agilis</i> sucking out a <i>Ceratium hirundinella</i> .	
- 8.	—	} empty carapaces with residua from the alimentary canal.	
- 9.	—		
- 10.	<i>Sacculus viridis</i>	amictic female seen dorsally	Obj. 4. Oc. 6
- 11.	—	amictic female seen ventrally	Obj. 4. Oc. 6
- 12.	—	amictic female seen laterally	Obj. 4. Oc. 6
- 13.	—	mictic female seen laterally	Obj. 4. Oc. 6
- 14.	—	male breaking out of the egg-shell	Obj. 4. Oc. 6
- 15.	—	male	Obj. 4. Oc. 6
- 16.	—	mouth parts	hom. Im. Oc. 6

## Plate V.

Fig. 1.	<i>Notops brachionus</i>	amictic female seen ventrally	Obj. 4. Oc. 4
- 2.	—	seen dorsally	Obj. 4. Oc. 4
- 3.	<i>Rhinops vitrea</i>	amictic female with two young ones	Obj. 16. Oc. 2
- 4.	—	mictic female with male eggs	Obj. 16. Oc. 2
- 5.	—	mictic female with resting egg	Obj. 16. Oc. 2

- Fig. 6—8. *Brachionus angularis*. Frederiksborg Castle Lake. Summer form (fig. 7) with a jelly coating and protruding posterior angles. . . . . Obj. 16. Oc. 4
- 9—38. *Brachionus pala*. Bistrup Pond . . . . . Obj. 16. Oc. 4
- Fig. 9—19. Seasonal variation in 1929; the species disappears from the plancton in Oktober 1929 as a typical *B. pala* and reappears again in the same shape in May 1930. Fig. 20—38 shows the seasonal variation till the stage Fig. 9 (22/VII 29) has been reached. The species is only represented as *pala* in May; forma *amphiceros* begins to appear in the beginning of June; from the beginning of July the forms with excessively long thorns appear. Figs. 35 and 36 show the mother animal; it carried an egg from which a young one fig. 36 b was born; the young one was drawn half an hour after birth; the posterior thorns are twice as long as those of the mother animal. Figs. 37 and 38 show two animals, fig. 37 represents a dead animal, fig. 38 a living animal when swimming; the posterior thorns are carried stretched out parallel with the long axis of the animal (see p. 115).
- 39—41. *Brachionus pala* the three kinds of egg . . . . . Obj. 16. Oc. 4

## Plate VI.

- Fig. 1. *Brachionus pala* mictic female with resting egg; seen ventrally . . . . . Obj. 4. Oc. 6
- 2. — a peculiar form from a pond near Sorø; mictic female with resting eggs seen ventrally . . . . . Obj. 4. Oc. 6
- 3. — resting egg deposited. Autumn.
- 4. — resting egg spring; the young one fully developed, posteriorly the air bubble.
- 5. — resting egg emptied but the shell still with the air bubble.
- 6. *Brachionus angularis* amictic female with two eggs. . . . . Obj. 16. Oc. 4
- 7. — mictic female not fertilized; carrying male eggs.
- 8. — mictic female fertilized; the ovary very dark, filled with oilglobules.
- 9. — mictic female; the resting egg formed.
- 10. — mictic female; carrying two resting eggs, the one a little older than the other.
- 11. — amictic female carrying two eggs and covered with amictic and male eggs of *Rattulus pusillus* of which a female is seen upon the carapace and a male swimming near it. . . . . Obj. 4. Oc. 6
- 12. — male of *Rattulus pusillus* contracted . . . . . Obj. 4. Oc. 6

## Plate VII.

- Fig. 1—5. *Anuræa aculeata*. Seasonal variation in Frederiksborg Castle Lake . . . . .
- 6—8. — Seasonal variation in M. Pond . . . . .
- 9—14. — Seasonal variation in Horseshoe Pond . . . . .
- 15—18. — Seasonal variation in Fredensborg Pond . . . . .
- 19—23. — Seasonal variation in Insel Pond . . . . .
- 24—33. — Seasonal variation in Nøddebo Pond . . . . .
- 34—38. — Seasonal variation in Schæffergaard Pond . . . . .
- 39—47. — Seasonal variation in Asminderød Pond . . . . .
- } Obj. 16. Oc. 4

## Plate VIII.

Fig. 1—21. <i>Anuræa cochlearis</i> Seasonal variation Funke Pond. Fig. 1—2, April 1910. Fig. 3—12, June 1910. Fig. 13—21, June 1923.	Obj. 16. Oc. 4
Fig. 22. <i>Gastropus hyptopus</i> amictic female	Obj. 4. Oc. 6
- 23. — amictic female, after starvation	Obj. 4. Oc. 6
- 24. — amictic female seen dorsally	Obj. 4. Oc. 4
- 25. — amictic female seen ventrally	Obj. 4. Oc. 4
- 26. — carapace seen dorsally	Obj. 4. Oc. 4
- 27. — resting egg	Obj. 4. Oc. 6
- 28. <i>Anapus testudo</i> seen ventrally	Obj. 4. Oc. 6
- 29. — seen dorsally	Obj. 4. Oc. 6
- 30. — mouth parts	Obj. 4. Oc. 12
- 31. <i>Anapus ovalis</i> seen ventrally	Obj. 4. Oc. 6

## Plate IX.

Fig. 1. <i>Gastropus stylifer</i> amictic female	Obj. 4. Oc. 6
- 2. — amictic egg	Obj. 4. Oc. 6
- 3. — <i>Uroglena volvox</i> with two eggs of <i>G. stylifer</i> .	
- 4. <i>Gastropus minor</i>	Obj. 4. Oc. 6
- 5. <i>Ploesoma triacantha</i>	Obj. 4. Oc. 6
- 6. — carapace seen laterally	Obj. 4. Oc. 6
- 7. — — dorsally	Obj. 4. Oc. 6
- 8. — — ventrally	Obj. 4. Oc. 6
- 9. — mouth parts	Obj. 4. Oc. 12
- 10. }	
- 11. } <i>Asplanchna Sieboldi</i> . Bistrup Pond. Seasonal variation	Obj. 16. "Sucherocular"
- 12. }	
- 13. — — — Male	Obj. 16. Oc. 6
- 14. — — — Resting egg	Obj. 16. Oc. 6
- 15. <i>Rattulus capuzinus</i> . Forepart; the wheelorgan withdrawn	Obj. 4. Oc. 4

## Plate X.

Fig. 1. <i>Ploesoma Hudsoni</i> amictic female seen ventrally	Obj. 4. Oc. 2
- 2. — — — seen dorsally	Obj. 4. Oc. 2
- 3. — — — laterally	Obj. 4. Oc. 2
- 4. — amictic pelagic egg	Obj. 4. Oc. 2
- 5. — — — —	Obj. 4. Oc. 2

## Plate XI.

Fig. 1. <i>Asplanchnopus myrmeleo</i> . Male; in the middle of the figure between the two large muscles the long rudiment of the alimentary canal with gastral glands	Wasserim. Oc. 6
- 2. <i>Synchaeta stylata</i> amictic female seen ventrally	Obj. 4. Oc. 6
- 3. — — — seen dorsally, to show the protuded mouth tube	Obj. 4. Oc. 4
- 4. — <i>pectinata</i> amictic egg	Obj. 4. Oc. 4

Fig. 5.	<i>Synchæta pectinata</i>	male egg	Obj. 4. Oc. 4
- 6.	—	resting egg	Obj. 4. Oc. 4
- 7.	<i>Polyarthra platyptera</i>	amictic female with egg	Obj. 4. Oc. 4
- 8.	—	male egg	Obj. 4. Oc. 4
- 9.	—	resting egg	Obj. 4. Oc. 4

## Plate XII.

Fig. 1.	<i>Asplanchna priodonta</i> .	Seasonal variation, Haldsø. The specimens from 9/VII show three generations inside each other	Obj. 16. "Sucherocular"
- 2.	—	<i>priodonta</i> genital organs female	Obj. 4. Oc. 6
- 3.	—	<i>Sieboldi</i> mouth parts	Waterimm. Oc. 6
- 4.	—	<i>Sieboldi</i> genital organs female	Obj. 4. Oc. 6
- 5.	—	<i>priodonta</i> mouth parts	Waterimm. Oc. 6
- 6.	—	<i>Brightwelli</i> . Old female with numerous embryos in uterus	Obj. 4. Oc. 2

## Plate XIII.

Fig. 1.	<i>Asplanchnopus myrmeleo</i> .	Male, seen dorsally	Obj. 4. Oc. 6
- 2.	<i>Asplanchna Brightwelli</i>	in Copula	Obj. 16. Oc. 4
- 3.	—	The male is lying free in the body cavity, after rupture of the uterus	Obj. 16. Oc. 4
- 4.	—	The female is dead and the male gets free, swimming away after the decomposition of the female	Obj. 16. Oc. 4
- 5.	<i>Triarthra brachiata</i>	amictic female	Obj. 4. Oc. 6
- 6.	—	mictic female with the large resting egg	Obj. 4. Oc. 6
- 7.	<i>Triarthra longiseta</i>	amictic female	Obj. 4. Oc. 6
- 8.	—	mictic female with resting egg	Obj. 4. Oc. 6
- 9.	—	mictic female with unripe resting egg	Obj. 4. Oc. 6
- 10.	—	ripe resting egg	Obj. 4. Oc. 6

## Plate XIV.

Fig. 1.	<i>Asplanchna priodonta</i>	from Hald lake	Obj. 16. Oc. 4
- 2.	—	from Frederiksborg Castle Lake	Obj. 16. Oc. 4
Fig. 2 represents the normal size and form of <i>A. priodonta</i> . Fig. 1 the abnormal pelagic form. The organs in the specimens from Hald Lake are not larger than those from Frederiksborg Castle Lake. It is especially the posterior part of the body which has been augmented in size.			
- 3.	<i>Triphylus lacustris</i>	female. The figure has been drawn to be compared with that of the almost unknown male. Though the species was regularly observed in 1929 and 1930 and many hundred females observed, only one single male was seen. The sketch could not be used for publication	Obj. 4. Oc. 2
- 4.	—	Mouth parts	Waterim. Oc. 6
- 5.	—	Summer egg	Obj. 16. Oc. 2
- 6.	<i>Lacinularia socialis</i>	mictic colony with male eggs, deposited in the jelly	Obj. a*. Obj. 16
- 7.	—	mictic colony with male eggs deposited in the jelly and resting eggs in the inside of the females	a*. Obj. 16

## Plate XV.

*Asplanchna priodonta*. The seasonal variation in Hald Lake. Camera drawings of the animals during the period 3/V (temperature 7) to 9/VII temperature 15. By 3/V the species is almost isodiametric, by 9/VII much longer than broad. The species occurs only as isodiametric forms on 3/V and 30/V, showing a slight prolongation of the longitudinal axis. The isodiametric form disappears totally in June. From the middle of June to the middle of July the longitudinal axis is regularly augmented, the transversal axis being almost unaltered. Compare also pag. 167. The table further shows that the young ones still lying in the mother animals show greater differences in the relation between the two axes than the mother animals.

The species disappears from the plankton in the forms shown in figs. 29—31 and does not reappear in the plankton until May the next year. Then the form is again isodiametric.

## Corrigenda.

p. 79. Heading	Notommata sp. Plate II, fig. 1—5	read	Notommata sp. Plate II, fig. 1—4.
p. 80. Heading	Notommata sp. Plate II, fig. 6	—	Notommata sp. Plate II, fig. 5.
p. 86. Lin. 10 from below	Tab. II, fig. 7	—	Tab. XI, fig. 3.
p. 111. Lin. 10 from below	Brachioninus	—	Brachionus.
p. 112. Heading	Br. pala Plate V, fig. 9—30	—	Br. pala. Plate V, fig. 9—41.
p. 115. Lin. 13 from above	Tab. V, fig. 9—30	—	Tab. V, fig. 9—19.
p. 128. Lin. 14 from above	fig. 15—18.	to be expunged	
p. 146. Heading	<i>Asplanchna Brightwelli</i> . Plate XII, fig. 2, 3, 6	read	<i>Asplanchna Brightwelli</i> . Plate XII, fig. 3—6.
p. 163. Heading	<i>Asplanchna priodonta</i> Plate XII, fig. 1, 5	—	<i>Asplanchna priodonta</i> . Plate XII, fig. 1, 2, 5.

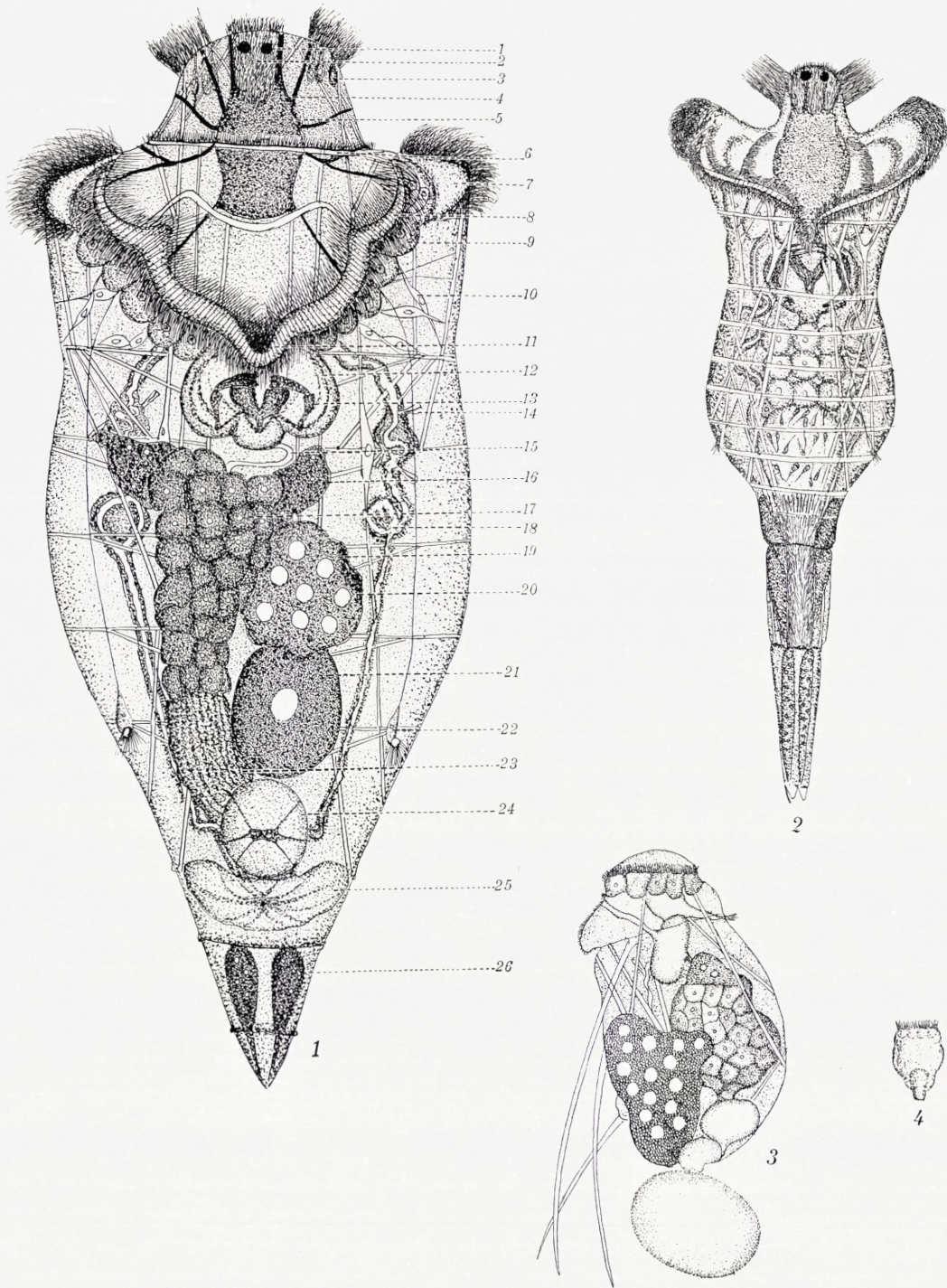


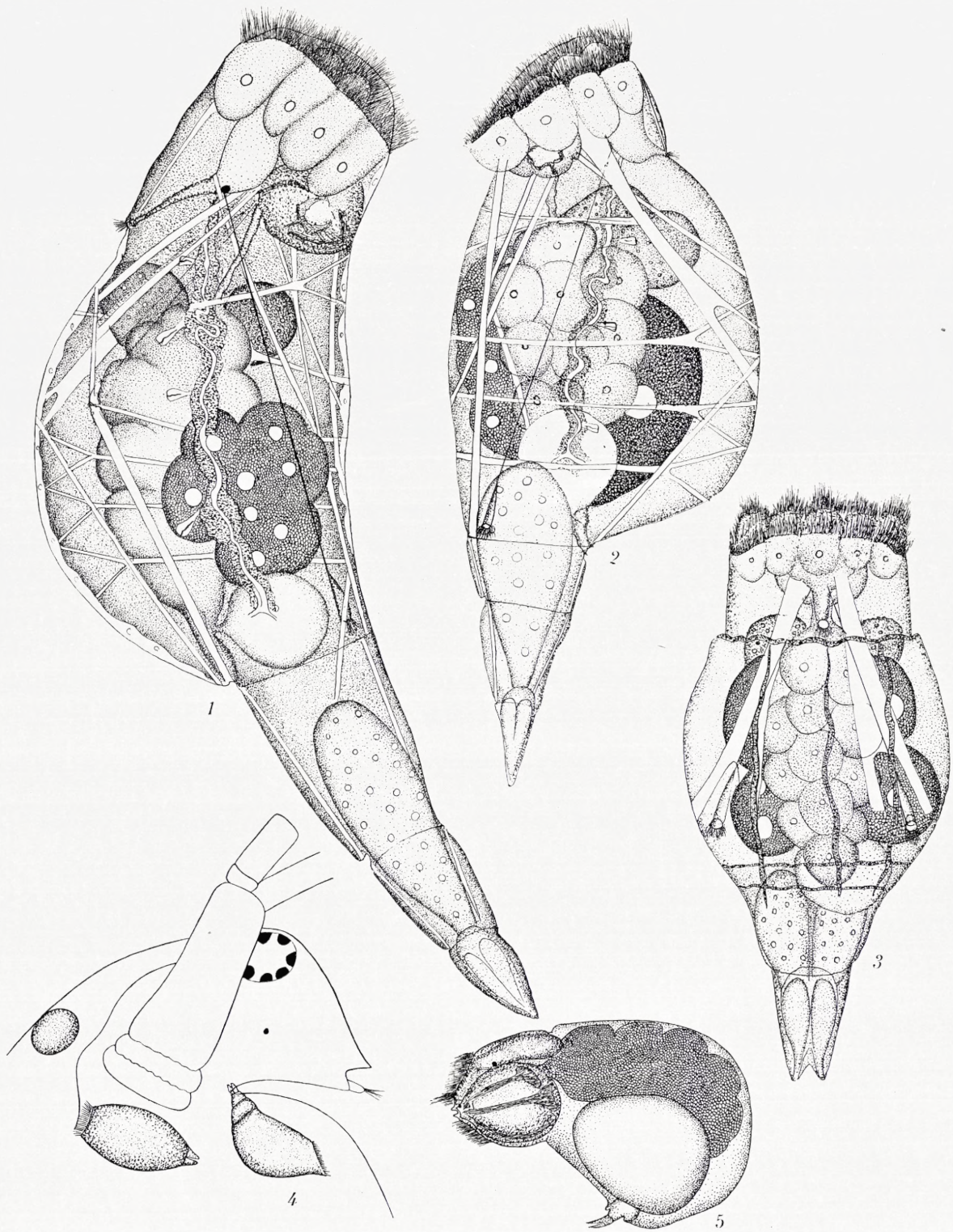


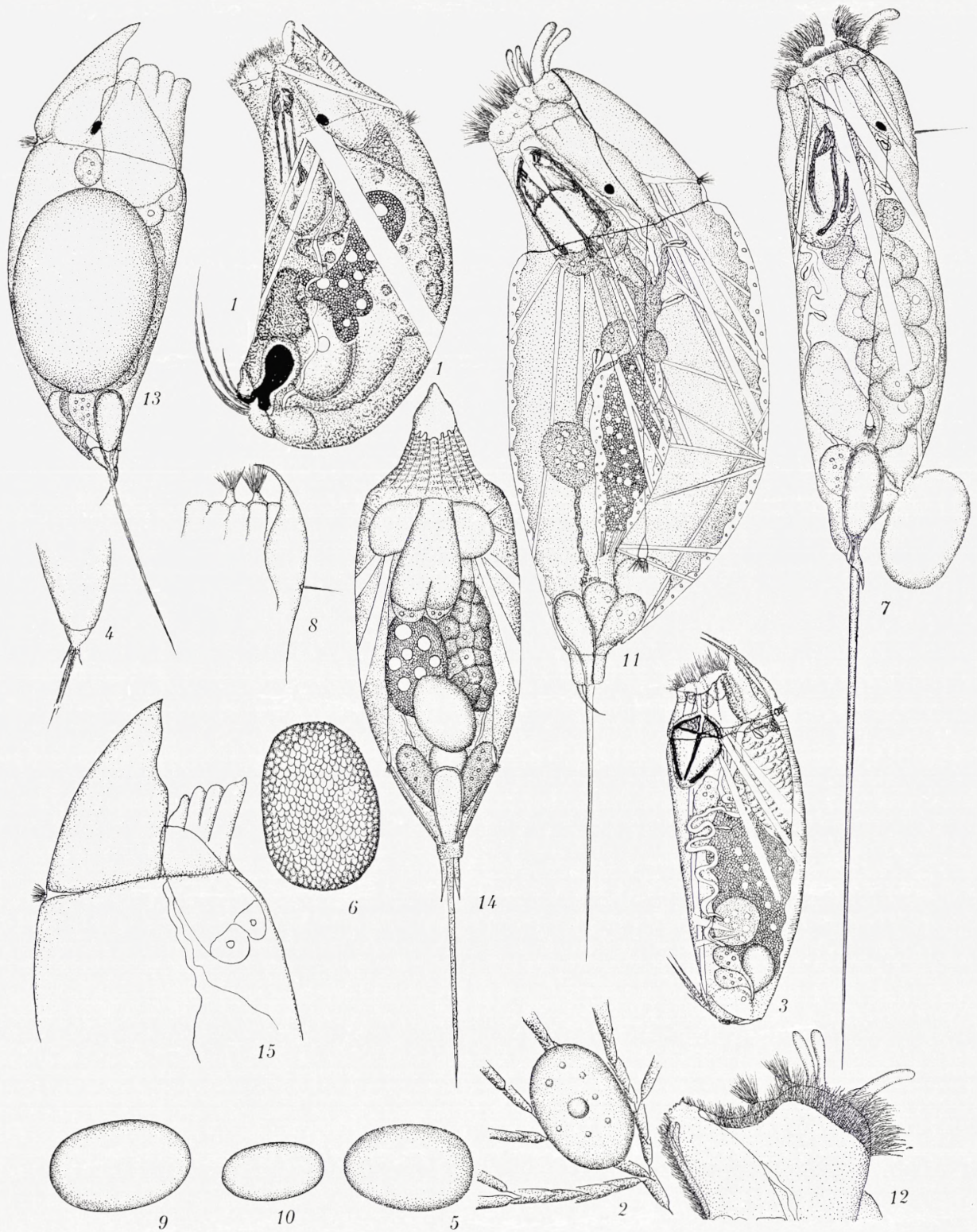


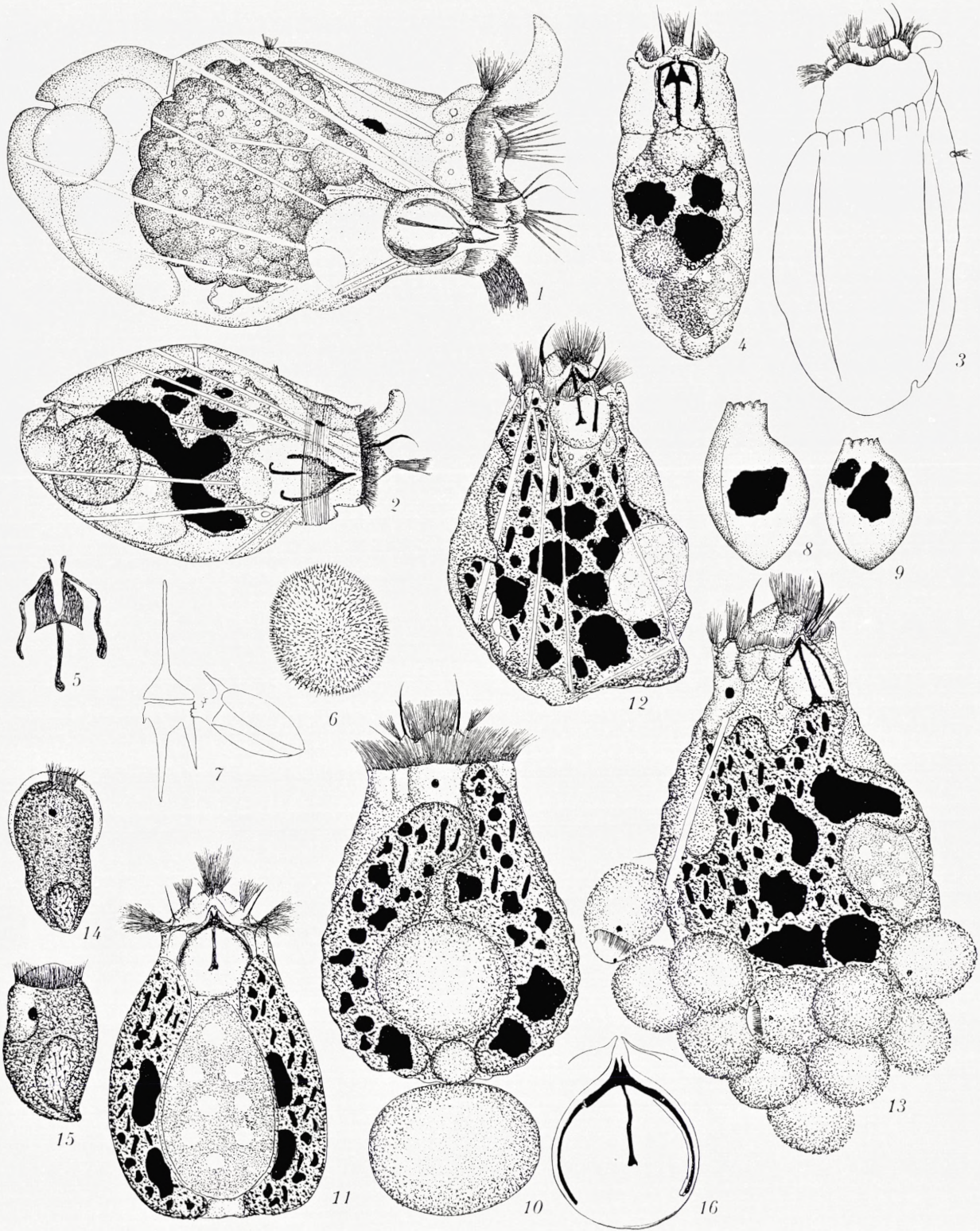




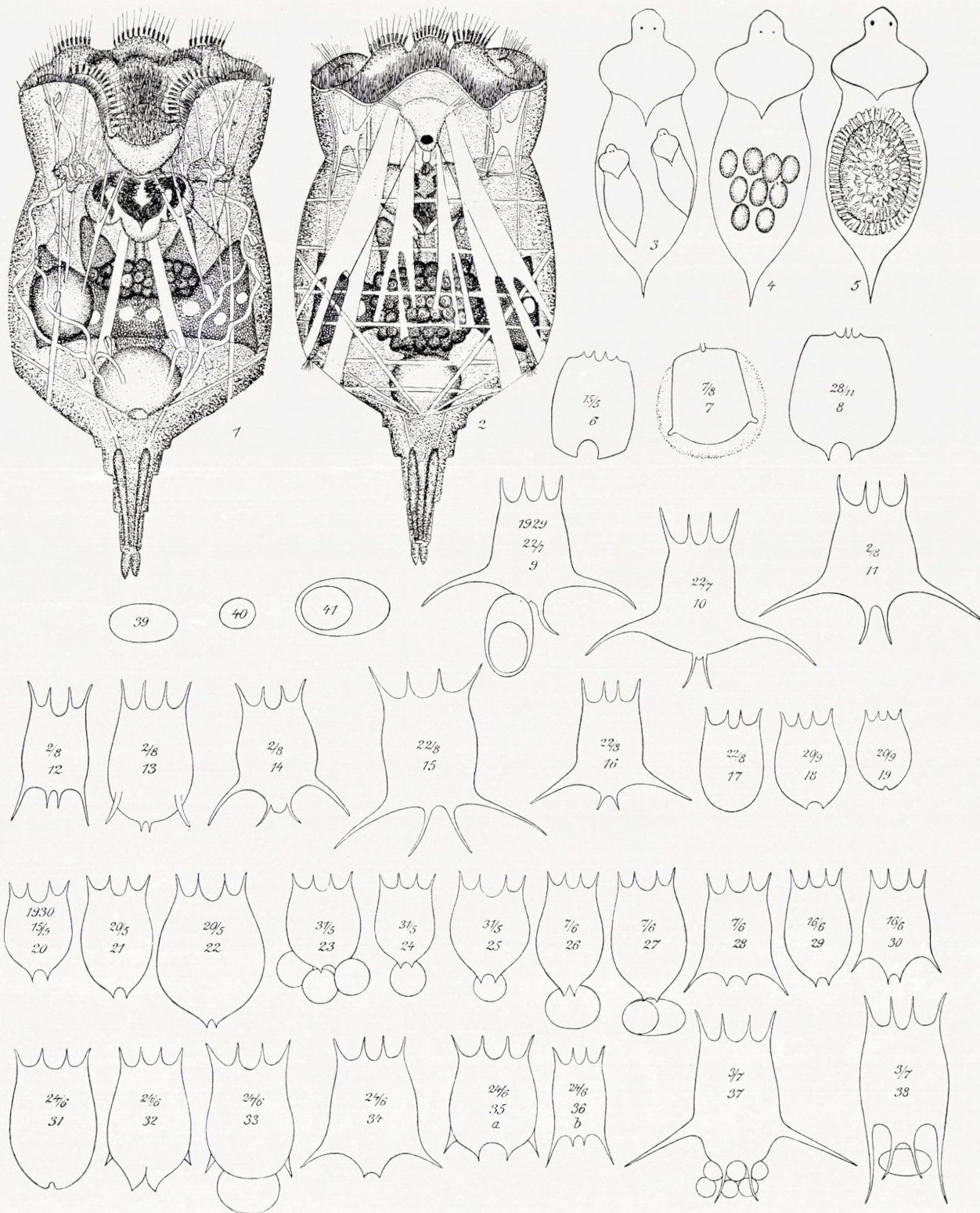


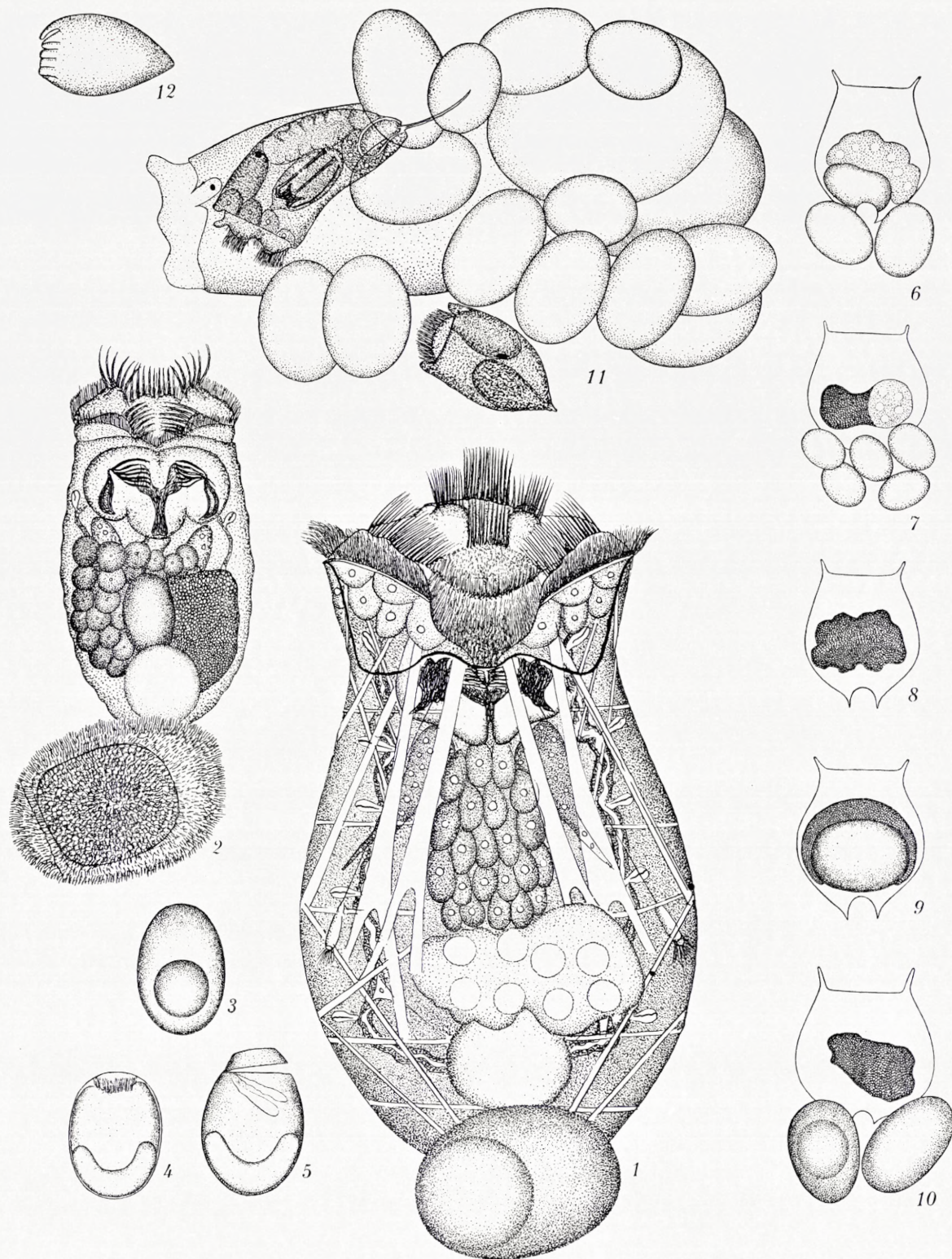




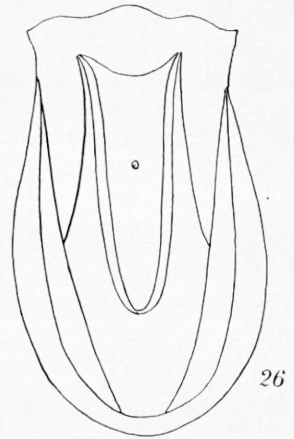
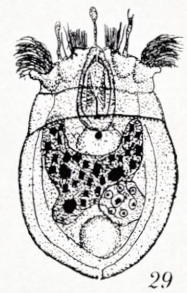
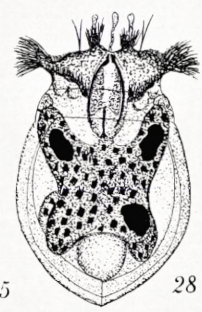
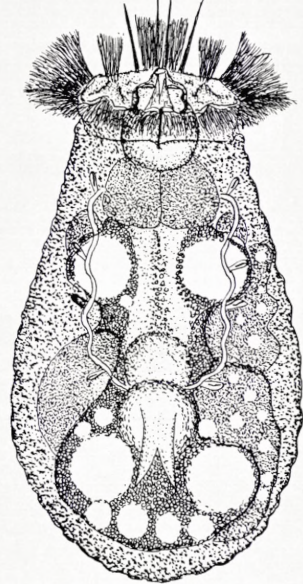
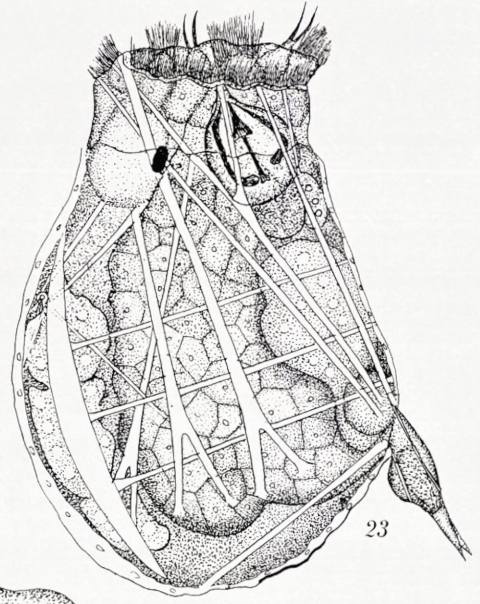
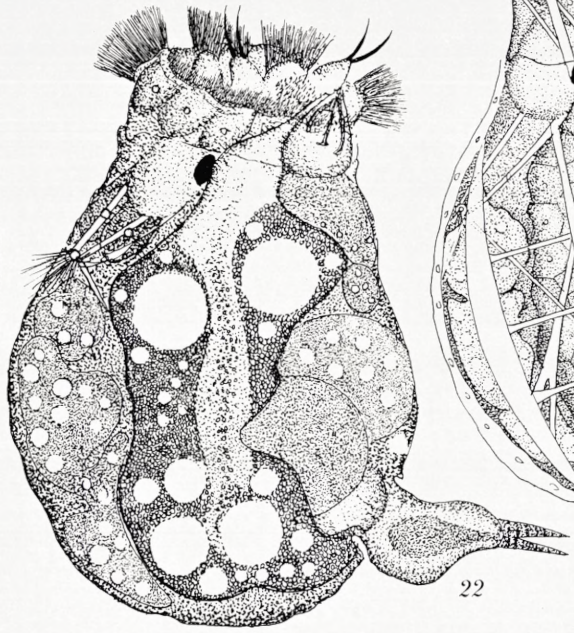
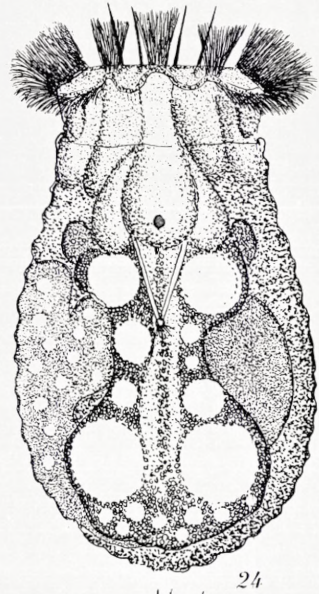
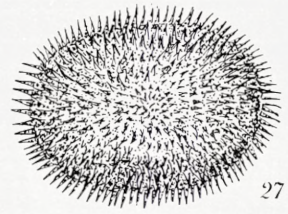


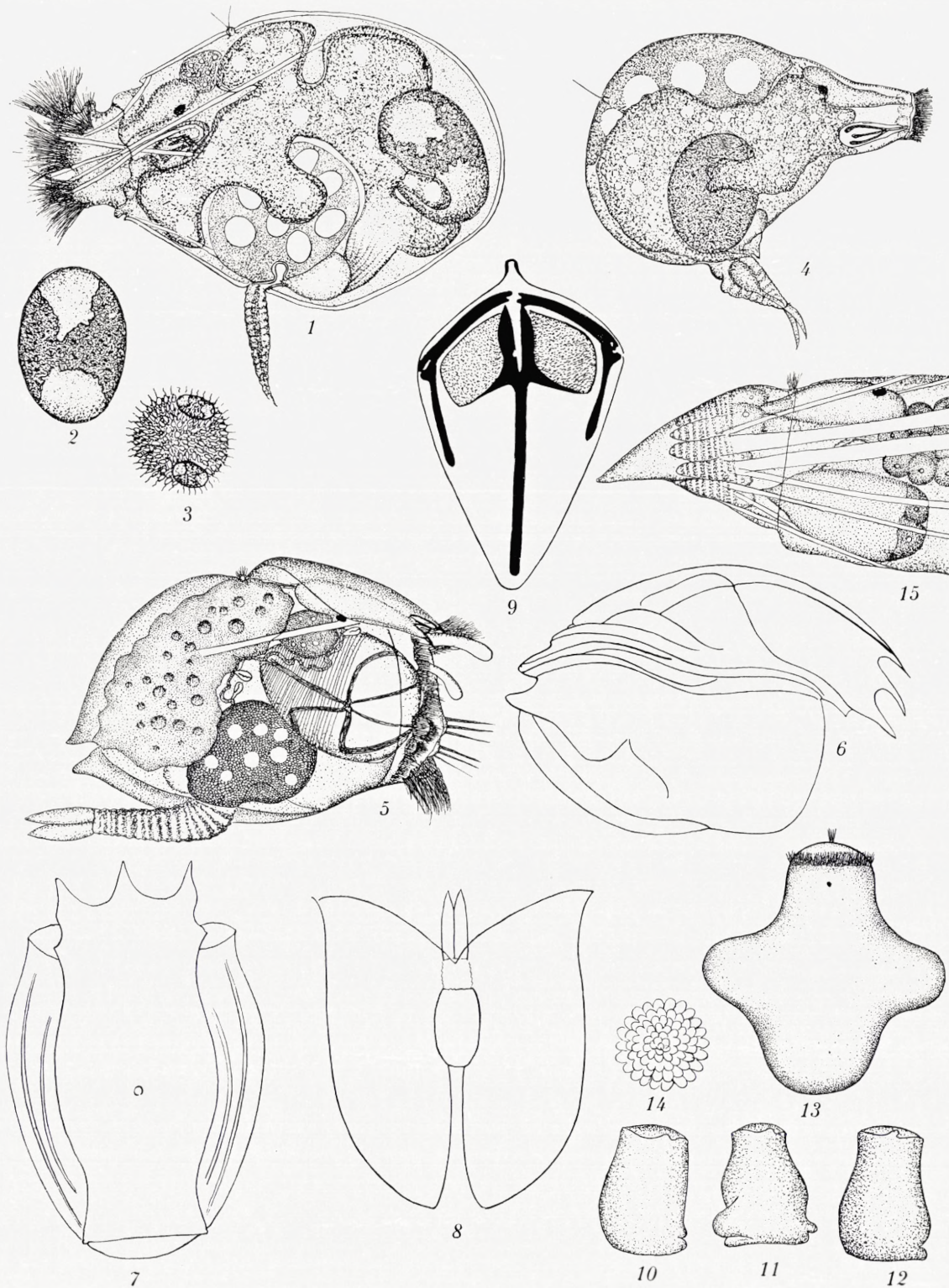


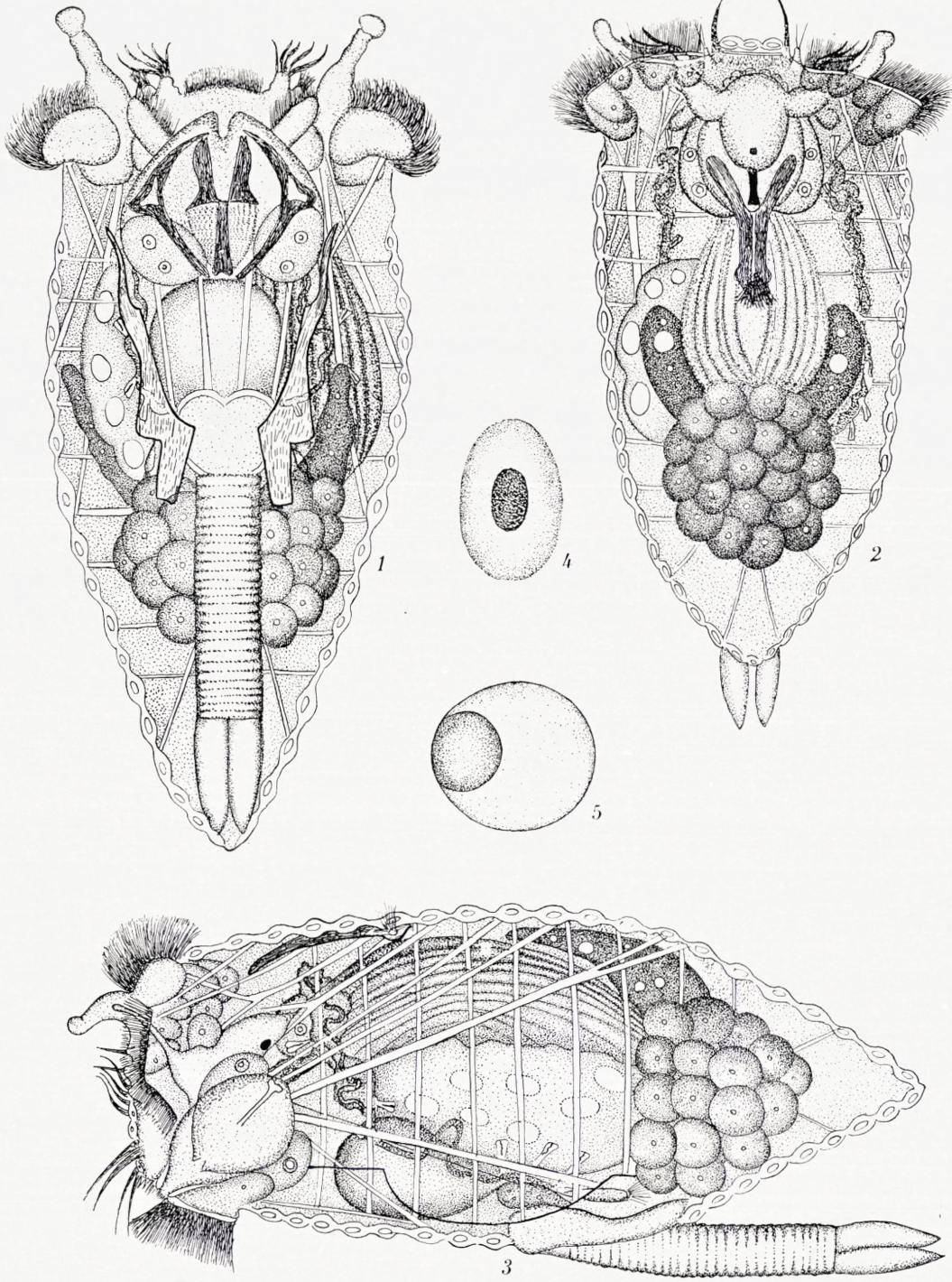


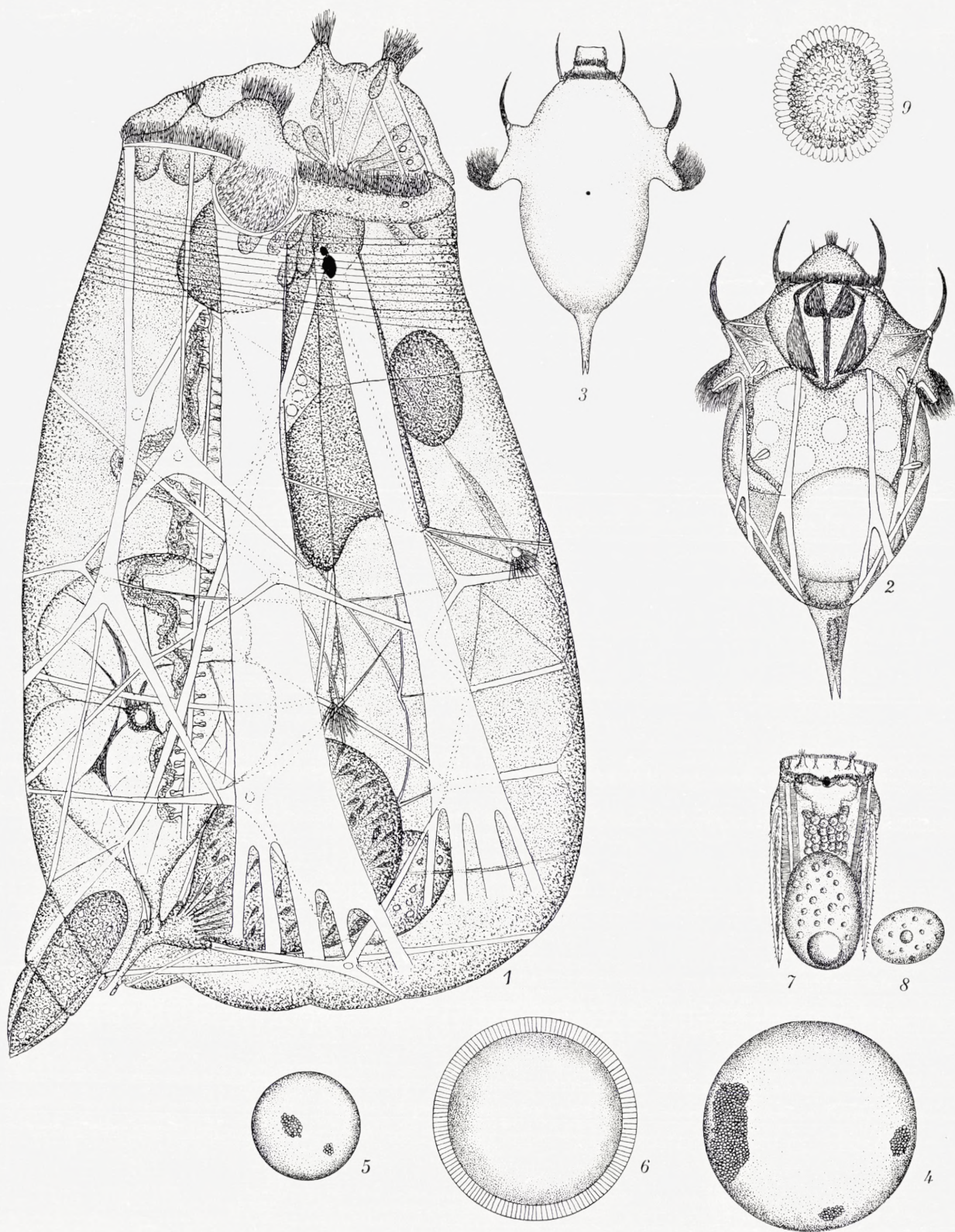


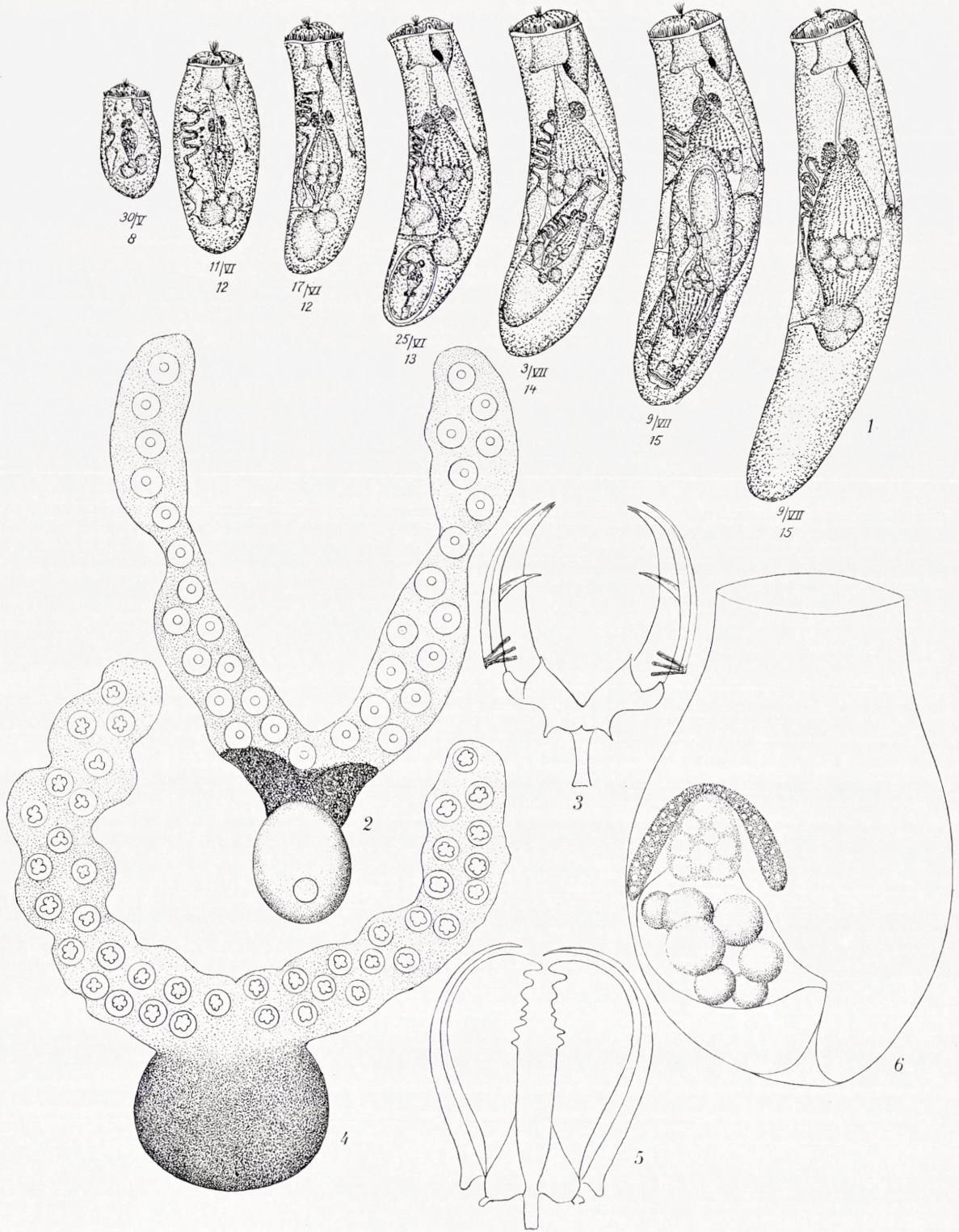




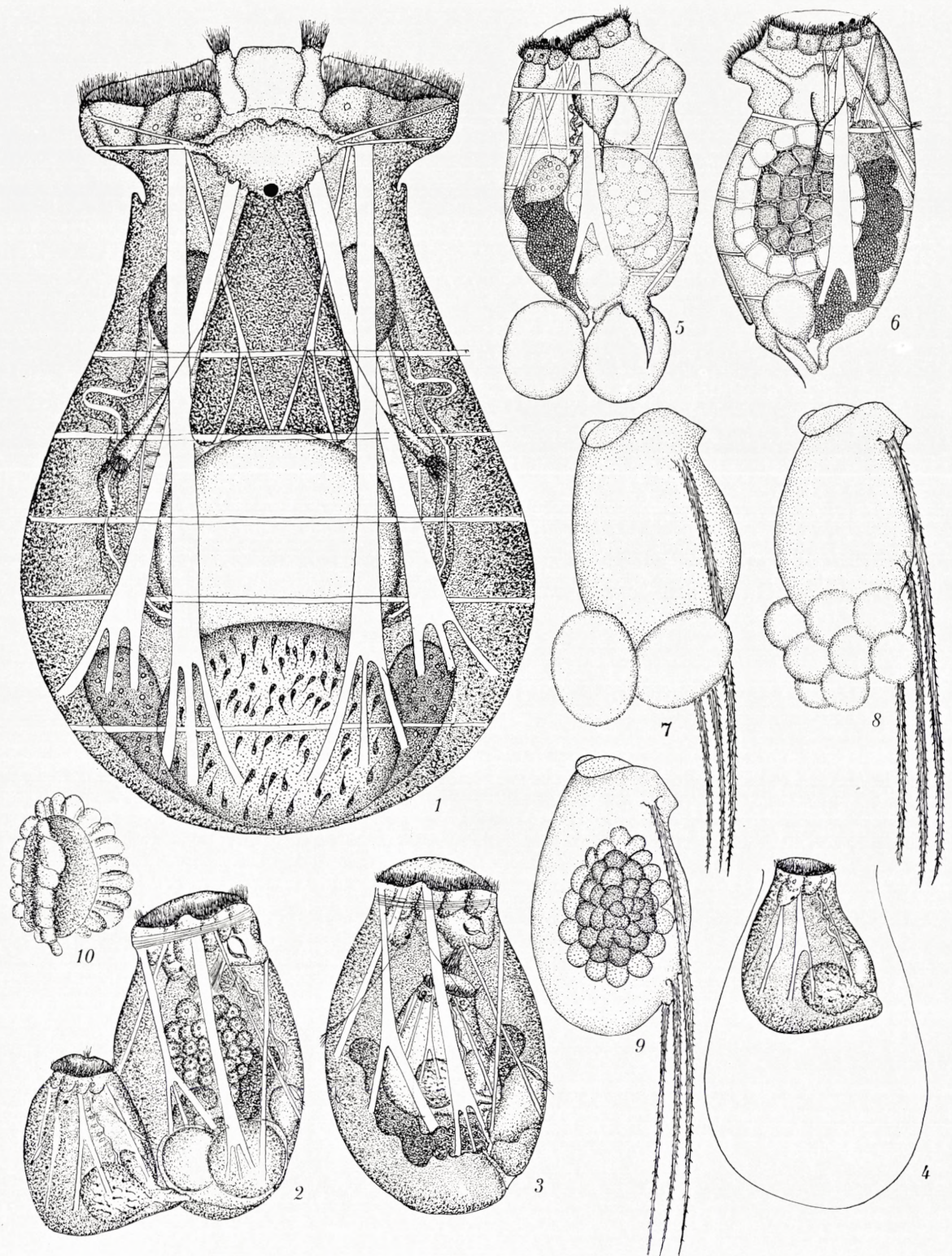


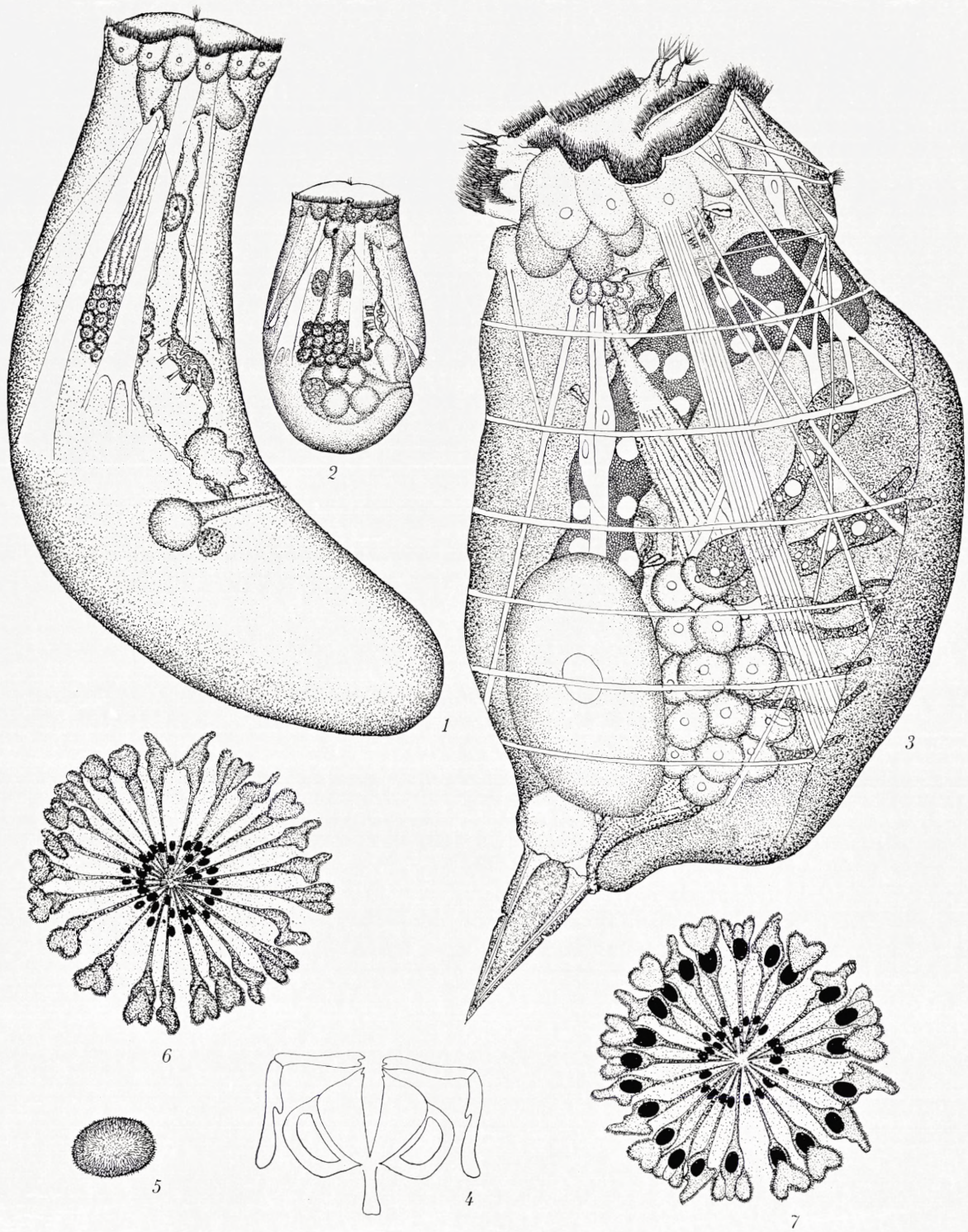




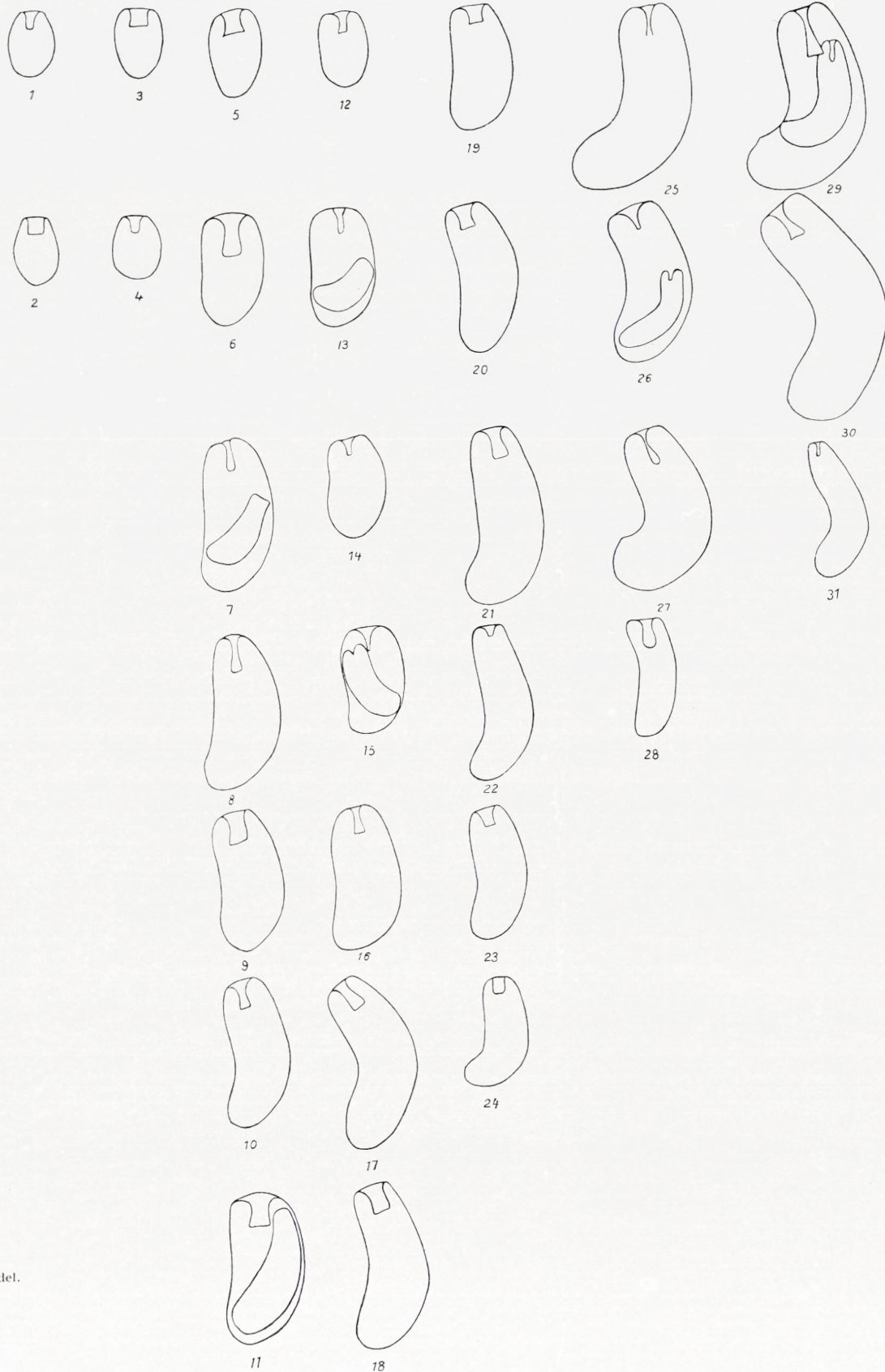








3/V	30/V	11/VI	17/VI	25/VI	3/VII	9/VII
7	8	12	12	13	14	15





Det Kgl. Danske Videnskabernes Selskabs Skrifter.  
Naturvidenskabelig og matematisk Afdeling,  
8de Række.

	Kr.	Øre
<b>I, 1915—1917</b> .....	10.	75.
1. <b>Prytz, K. og J. N. Nielsen:</b> Undersøgelser til Fremstilling af Normaler i Metersystemet, grundet paa Sammenligning med de danske Rigsprototyper for Kilogrammet og Meteren. 1915.....	1.	55.
2. <b>Rasmussen, Hans Baggsgaard:</b> Om Bestemmelse af Nikotin i Tobak og Tobaksextrakter. En kritisk Undersøgelse. 1916 .....	1.	75.
3. <b>Christiansen, M.:</b> Bakterier af Tyfus-Coligruppen, forekommende i Tarmen hos sunde Spædkalve og ved disses Tarminfektioner. Sammenlignende Undersøgelser. 1916 .....	2.	25.
4. <b>Juel, C.:</b> Die elementare Ringfläche vierter Ordnung. 1916 .....	3.	60.
5. <b>Zeuthen, H. G.:</b> Hvorledes Mathematiken i Tiden fra Platon til Euklid blev en rationel Videnskab. Avec un résumé en français. 1917.....	8.	00.
<b>II, med 4 Tavler, 1916—1918</b> .....	11.	50.
1. <b>Jørgensen, S. M.:</b> Det kemiske Syrebegrebs Udviklingshistorie indtil 1830. Efterladt Manuskript, udgivet af <i>Ove Jørgensen</i> og <i>S. P. L. Sørensen</i> . 1916 .....	3.	45.
2. <b>Hansen-Ostenfeld, Carl:</b> De danske Farvandes Plankton i Aarene 1898—1901. Phytoplankton og Protozoer. 2. Protozoer; Organismer med usikker Stilling; Parasiter i Phytoplanktonter. Med 4 Figurgrupper og 7 Tabeller i Teksten. Avec un résumé en français. 1916 .....	2.	75.
3. <b>Jensen, J. L. W. V.:</b> Undersøgelser over en Klasse fundamentale Uligheder i de analytiske Funktioners Theori. I. 1916.....	3.	90.
4. <b>Pedersen, P. O.:</b> Om Poulsen-Buen og dens Teori. En Experimentalundersøgelse. Med 4 Tavler. 1917 .....	2.	90.
5. <b>Juel, C.:</b> Die gewundenen Kurven vom Maximalindex auf einer Regelfläche zweiter Ordnung. 1917 .....	3.	75.
6. <b>Warming, Eug.:</b> Om Jordudløbere. With a Résumé in English. 1918 .....	3.	65.
<b>III, med 14 Kort og 12 Tavler, 1917—1919</b> .....	26.	00.
1. <b>Wesenberg-Lund, C.:</b> Furesøstudier. En bathymetrisk Undersøgelse af Mølleaaens Søer. Under Medvirkning af Oberst <i>M. J. Sand</i> , <i>Mag. J. Boye Petersen</i> , <i>Fru A. Seidelin Raunkjær</i> og <i>Mag. sc. C. M. Steenberg</i> . Med 7 bathymetriske Kort, 7 Vegetationskort, 8 Tavler og ca. 50 i Teksten trykte Figurer. Avec un résumé en français. 1917 .....	22.	00.
2. <b>Lehmann, Alfr.:</b> Stofskifte ved sjælelig Virksomhed. With a Résumé in English. 1918 .....	3.	15.
3. <b>Kramers, H. A.:</b> Intensities of Spectral Lines. On the application of the Quantum Theory to the problem of the relative intensities of the components of the fine structure and of the stark effect of the lines of the hydrogen spectrum. With 4 plates. 1919 .....	9.	50.
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1. <b>Bohr, N.:</b> On the Quantum Theory of Line-Spectra. Part I. 1918 .....	2.	25.
— Samme. Part II. 1918 .....	4.	00.
— — — III. 1922 .....	1.	25.
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<b>VI</b> , med 12 Tavler .....	25.	70.
1. <b>Christensen, Carl</b> : A Monograph of the genus <i>Dryopteris</i> . Part II. 1920.....	8.	25.
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3. <b>Børgesen, F.</b> : Contributions to the knowledge of the Vegetation of the Canary Islands (Teneriffe and Gran Canaria). With an appendix: Lichenes Teneriffenses, scripsit Edv. A. Wainio. 1924.....	7.	50.
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1. <b>Wesenberg-Lund, C.</b> : Contributions to the Biology of the Danish Culicidæ. With 21 Plates and 19 Figures in the text. 1920—21 .....	29.	00.
2. <b>Nørlund, N. E.</b> : Stirlings Interpolationsrække. 1924 .....	4.	50.
3. <b>Levinsen, G. M. R.</b> : Undersøgelser over Bryozoen i den danske Kridtformation. Efter Forfatterens Død udgivet af Dr. K. Brünnich Nielsen og Dr. Th. Mortensen. Med 8 Tavler. 1925.....	16.	50.
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<b>Jessen, Knud og Jens Lind</b> : Det danske Markkruddts Historie. Med 1 Oversigtsskema. 1922—23.	24.	50.
<b>IX</b> , med 5 Tavler.		
<b>Thoroddsen, Th.</b> : Die Geschichte der isländischen Vulkane (nach einem hinterlassenen Manuskript). Mit 5 Tafeln. 1925.....	25.	15.
<b>X</b> , med 30 Tavler og 2 Kort .....	38.	10.
1. <b>Wesenberg-Lund, C.</b> : Contributions to the Biology of <i>Zoothamnium Genticulatum</i> Ayrton. With 14 Plates. 1925.....	14.	00.
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4. <b>Johs. Schmidt</b> : On the distribution of the Fresh-Water Eels ( <i>anguilla</i> ) throughout the world. II. Indo-pacific region. A bio-geographical investigation. With two charts and ten text-figures. 1925.	5.	00.
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1. <b>Luplau Janssen, C.</b> : La Surface de la Planète Jupiter 1919—1924. Avec 7 planches. 1926.....	10.	00.
2. <b>Wesenberg-Lund, C.</b> : Contributions to the Biology and Morphology of the Genus <i>Daphnia</i> with some Remarks on Heredity. With 2 Plates and 21 Textfigures. 1926.....	13.	20.
3. <b>Braae, Johannes</b> : Eine Reihe differentieller Beobachtungen am Meridiankreis der Kopenhagener Universitätssternwarte. 1927.....	5.	00.
4. <b>Ravn, J. P. J.</b> : De irregulære Echinider i Danmarks Kridtfaejringer. Med 5 Tavler. 1927.....	6.	00.
5. <b>Mortensen, Th.</b> : On the Postlarval Development of some <i>Cidarids</i> . 1927.....	2.	00.
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1. <b>Kramp, P. L.</b> : The Hydromedusæ of the Danish Waters. 1927.....	16.	50.
2. <b>van den Bos, W. H.</b> : The Multiple System § Ursæ Majoris. 1928.....	2.	50.
3. <b>Bohr, Harald og Jessen, Børge</b> : Om Sandsynlighedsfordelinger ved Addition af konvekse Kurver. Med 34 Figurer. 1929 .....	8.	60.

### 9de Række.

<b>I</b> , med 35 Tavler .....	30.	50.
1. <b>Ravn, J. P. J.</b> : De regulære Echinider i Danmarks Kridtfaejringer. Med 6 Tavler. 1928 .....	7.	00.
2. <b>Clausen, Hans</b> : On the Crystal Structure of Cryolithionite. With 4 Figures in the text. 1928 ..	2.	25.
3. <b>Boas, J. E. V.</b> : Biologisch-anatomische Studien über den Hals der Vögel. Mit 23 Tafeln und 20 Figuren im Text. 1929.....	20.	00.
4. <b>Berg, Kaj and Gunnar Nygaard</b> : Studies on the Plankton in the Lake of Frederiksborg Castle. With 6 Plates and 27 Figures in the text. 1929 .....	11.	50.
<b>II</b> , under Pressen:		
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