

CONTRIBUTIONS
TO
THE BIOLOGY AND MORPHOLOGY
OF THE GENUS DAPHNIA

WITH SOME REMARKS ON HEREDITY

BY
C. WESENBERG-LUND

WITH 2 PLATES AND 21 TEXTFIGURES

D. KGL. DANSKE VIDENSK. SELSK. SKRIFTER, NATURVIDENSK. OG MATHEM. AFD., 8. RÆKKE, XI. 2.



KØBENHAVN

HOVEDKOMMISSIONÆR: ANDR. FRED. HØST & SØN, KGL. HOF-BOGHANDEL

BIANCO LUNOS BOGTRYKKERI

1926

Pris: 13 Kr. 20 Øre.

CONTRIBUTIONS
TO
THE BIOLOGY AND MORPHOLOGY
OF THE GENUS DAPHNIA

WITH SOME REMARKS ON HEREDITY

BY

C. WESENBERG-LUND

WITH 2 PLATES AND 21 TEXTFIGURES

D. KGL. DANSKE VIDENSK. SELSK. SKRIFTER, NATURVIDENSK. OG MATHEM. AFD., 8. RÆKKE, XI. 2.



KØBENHAVN

HOVEDKOMMISSIONÆR: ANDR. FRED. HØST & SØN, KGL. HOF-BOGHADEL

BIANCO LUNOS BOGTRYKKERI

1926

Introduction.

When after more than ten years' study of the plancton of the Danish lakes I published my Plancton Investigations in 1908, I had upon numerous excursions gathered very many observations relating partly to the biology of freshwater insects partly to the propagation of the Rotifera. The first named observations have now been published in a rather long series of publications, and those on the Rotifera, the first part of which has been published, will soon be finished.

Like all more extensive explorations, the Plancton Investigations raised very many unsolved problems, many of which were pointed out by myself. Many of them have occupied my thoughts in the time from 1908 till now, and moreover, I have in different ways tried to get material for their solution.

Already in 1899 I shared the view that the Rotifera were originally creeping organisms bound to the bottom vegetation, and that several of them could be arranged in a series of parallel developmental lines all deriving from the creeping littoral *Notommatidae*; their original home was to be found in the freshwater and not in the sea (ZELINKA). Secondly the organisation of the Rotifera has been altered in such a way that from creeping organisms they have been changed into freeswimming creatures more or less independent of the substratum, in the aberrant forms true plancton organisms.

In 1904 (p. 78) it was pointed out that when the plancton-diatoms *Asterionella gracillima*, *Tabellaria fenestrata*, *T. flocculosa* and *Diatoma elongatum* disappear from the plancton in late spring, it is always as stars, but when they reappear next spring, in March, it is chiefly as chains. It was therefore possible that these plancton organisms were recruited every year from forms which were attached to some substratum, and that these diatoms consequently changed between a chain-forming stage when they occurred attached to the substratum and a star-forming pelagic stage; during winter the stones of the Furesø are covered with thick greenish black coatings of chains of *Tabellaria* and *Diatoma*; these coatings are scraped off by the ice when this is broken during spring gales and, in the following weeks, found spread in the water layers all over the lake, the supposition was therefore justifiable, at all events as a working-theory for further investigations.

I 1904 (p. 185—188) I tried to show that WEISMANN'S view that *Leptodora hya-*

lina must be a very old form, an "Urdaphnide" (1874 p. 59) was the opposite of what was really the case; further that the systematic division of the *Cladocera* in *Calyptomera* and *Gymnomera* (G. O. SARS) was incorrect. The *Cladocera* should be arranged in developmental lines quite like the *Rotifera*. Their native home is the littoral zone and the vegetation where the lines begin; the most primitive forms are to be found in the *Lynceidæ*. One of these developmental lines begins with *Latona*; passing through *Sida* found in the pelagic region of Zürichersee (BALLY 1908 p. 148 and HEUSCHER 1917 p. 61), *Sida limnetica* (Lake of Geneva: BURCKHARDT 1900 p. 423), *Limnosida*, *Diaphanosoma*, the line finishes with *Leptodora* which is merely a member of the fam. *Sididae* modified for a pelagic life. It has no affinity to *Polyphemus* and *Bythotrephes* which belong to another developmental line; the explorations of LILLJEBORG (1900 p. 222) relating to *Bosmina globosa* (1900 p. 304) showed that a third line could be shown for the *Bosminidæ*; further on a fourth for the Daphnids.

With regard to the Daphnids (1908 p. 323) I wrote: "From the clumsy, strongly coloured pond and pool forms of the genus *Daphnia* with vigorous clinging and crawling apparatus, teeth on the terminal claws of the postabdomen, we have the races with slender, hyaline toothless claws of *D. hyalina* and *Hyalodaphnia*". WOLTERECK and his pupils, especially WAGLER, have later on come to the same result.

Later on LANGHANS (1909 p. 172 and 1911) and LITHINSKY (1916 a p. 252 and 1916 b p. 3) have adopted these views with regard to *Leptodora*, and in his last work WOLTERECK (1920 p. 30) has adopted almost the same lines as I carried on already in 1904; he added the line *Podon* — *Evadne* for the marine species. Among the insects I traced another developmental line in the Culicid larvæ: *Culex*, *Mochlonyx*, *Corethra*, the only insect larva which could be said to live a fully pelagic life (1908 p. 513).

Finally in 1908 in my Plancton Investigations Chap. XIII, Origin of the Freshwater Plancton (p. 321), the view was emphasized that the freshwater plancton could be designated as bottom and littoral forms which have adapted themselves more or less to pelagic life, and made themselves independent of bottom and bank where the great majority still pass a shorter or longer period of their life (as resting stages). The home of the freshwater plancton is to be found on the bottom and in the littoral region of the lakes whence it is still recruited to this very day. The view was opposed to that of PAVESI who supposed that the plancton was of marine derivation, and was inclined to regard all lakes with plancton as relict lakes (1880 p. 151). Before 1908 the above-named view was met with now and then in literature, although so far as I know only vaguely advanced (see especially ZACHARIAS (1893 p. 31). The hypothesis of the origin of the freshwater plancton set forth in the Plancton Investigations has been adopted later on by most investigators; PAVESI'S view holds good for only a few members of the community of freshwater plancton, especially for the *Diaptomidæ*.

In the following years it was evident to me that many of the problems which had arisen during my plancton investigations should be studied and traced back to

the littoral region, or better to the smaller lakes and ponds. With these problems in mind I have in 1910—1925 gathered a lot of biological observations relating to our freshwater fauna. In the years 1922—25 regular explorations have been carried on in a series of ponds and smaller lakes lying near my laboratory. In this way series of samples from different localities have accumulated; combined with other series from earlier years the whole collection now counts over 900 numbers.

From 1908 up to now many of these problems which the Plancton Investigations had brought forward were fortunately taken up by other naturalists with a different training and education. In many respects this has been of the greatest advantage for planctology. For myself it has been a great satisfaction that I have been able to help these investigators in different ways with material from my area of exploration; this holds good especially for the school of plancton investigations which, under the leadership of Prof. WOLTERECK, has produced a long series of papers, mainly relating to the biology of the genus *Daphnia*. Some of these investigators have visited this laboratory in the summer months, the leader himself pretty often.

Occupied as I have been with studies relating to the biology of Insects and Rotifera, the vast literature which has appeared in the time from 1908 up to now has been quite unknown to me. Having now arrived at the moment when I am to try to collect all my own observations, and my ideas relating to plancton problems of different kind noted down in the form of a diary, I have forced myself to read through this enormous literature, no inconsiderable part of which consists of German dissertations of which about fifteen alone derive from the University of Leipzig. On commencing the study of this enormous literature, my first thought was that in many of these areas of exploration science should now really have said her final word; later on I confess I arrived at another opinion. The main results of all these dissertations were mainly in accordance with the views of their professors. In this way a compact opinion against some of my leading views was created. These numerous explorations have brought forward very many valuable special observations, and have in a very high degree augmented our knowledge of the biology of the *Cladocera*; on the other hand, when these same observations were to be used to support considerations set forth not so much by the authors themselves as by their teacher, I fear that the future will show that upon that point they have to a higher degree retarded than promoted science. —

When it has been rather an easy matter to create this compact opinion against my views, it may be admitted that this is partly my own fault. Shortly after the publication of the Plancton Investigations my good friend Dr. Gunnar Andersson of Stockholm asked me if I would write a short account for the Swedish periodical "Ymer" of the main results of my studies. I never thought that this little paper, half popular in form as it was, would in the following years be translated into four other languages and be used to the extent that it was. I regret that limnologists have given so much consideration to this little paper and so little to the main work. In the

small paper, "Grundzüge" above 600 pages of large quarto were to be abbreviated to 44 pages octavo.

The above-named observations and collections from ponds and smaller lakes in my area of explorations were to result in a series of publications which have been planned during the last fifteen years and which will be carried on with due regard to the above-named literature. The first of these publications appears here.

In some of the ponds regular explorations have been carried on for some years with the special object of elucidating a series of questions set forth in the Plancton Investigations, all relating to the seasonal variation and propagation of the planctonic races of the genus *Daphnia*.

For a long time I have been of opinion that contributions to the solution of these questions could best be sought for when studying the species or races which belonged, not to the pelagic region of larger lakes, but to ponds and smaller lakes; this part of the explorations could not be carried on satisfactorily simultaneously with the explorations of the lake races. As well known WAGLER a. o. have been of quite the same opinion; in his excellent main work of 1912 WAGLER has shown how correct this view really was. In the work now published the results of my own new explorations will be given; on the basis of them a consideration of the plancton literature of 1908—1924 and its relation to my own plancton investigations of 1908 will be attempted.

Following the systematic which has been founded by KEILHACK (1909 p. 19) and more thoroughly worked out by WAGLER (1912 p. 344 a. flg.) I have in Denmark found four species of the genus *Daphnia*: *Daphnia magna* Straus (= *D. Schöfferi* Schödler), *D. pulex* (De Geer), *D. longispina* O. F. M. and *D. cucullata* G. O. Sars. *D. longispina* may be divided into two subspecies subsp. *longispina* and subsp. *hyalina*, and *D. cucullata* also in two subsp. *D. cucullata* and *D. cristata*. With regard to earlier authors the reader is particularly referred to WAGLER's paper. — WAGLER has referred all races treated in the Plancton Investigations to the two species *D. longispina* subsp. *longispina* and *D. cucullata* subsp. *cucullata*. In our lakes *D. cucullata* subsp. *cristata* has never been found; also *D. longispina* subsp. *hyalina* has hitherto never been recorded in our lakes.

According to the new nomenclature it would be most correct to refer *D. longispina* var. *pellucida* from Sorø and Tjustruplake to *D. longispina* subsp. *hyalina*.

From my own explorations, with due reference to the literature especially to that from the year 1908 to the present time, I will try to give a sketch of the main points in the anatomy and biology of our *Daphnia* species compared with the habitat and special conditions under which the animals are found.

Special Part.

Daphnia magna Straus.

In our country *D. magna* has always been found in very small pools and ditches, often in such as have only a diameter of 10—50 m; the depth is always extremely small, most probably not more than $\frac{1}{2}$ m, and often only with a few centim. of water. The bottom is covered with fine, commonly yellowish brown mud; the water itself is extremely rich in organic matter; it often smells nasty, and during summer it is overfilled with *Cyanophyceae*. In dry summers the water often disappears totally; in cold winters the ponds freeze to the bottom. In mild winters they are open; the *Cyanophyceae* have disappeared, but various *Chlorophyceae*, e. g. *Scenedesmus*, give the watermasses a green colour. Strong winds and heavy showers raise the bottom and change the colour to grey. The ponds often belong to the category waterpools and in summer harbour numerous ducks and geese. When dried up the bottom may be covered with grass, upon which the same birds and other small domestic animals throw their excrements. More than once small ditches have been found red with *D. magna* upon commons, rich in cattle, and near gates where the cattle were commonly gathered, and the pools were brown and partly consisted of urine. —

As well known, *D. magna* is the largest of all our Daphnids; it may reach a length of about 5—6 mm, more than *Limnetis brachyura*; the valves are almost as high as long and often so strongly vaulted that the whole animal is almost globular; the head is extremely flattened, often less than one fourth of the length of the valves, the rostrum is extremely blunt, the first pair of antennæ placed wide apart from the apex of the rostrum; the contours of the head are almost the same in all ponds, at all ages and at all seasons of the year; at all events, the variations are insignificant.

Of all our *Daphnia* species *D. magna* has the most highly developed fornices, they are strongly vaulted and between them and the dorsal contour run two conspicuous keels, which are admirably represented in the old figures of SCHÄFFER (1763 Tab. I fig. 6—7), of all figures those which best characterise the animal. These keels we do not find in any other of the *Daphnia* species; at all events they are but slightly developed. The globular valves demand strongly developed fornices, and the keels may most probably be regarded as staying lines. The spine is always short, only about $\frac{1}{4}$ of the length of the valves, it is straight, and may often be totally absent; according to HAACK (1915 p. 72) the spine does not increase. It remains at the stage which it had when the animal was born; often it totally disappears; this is perhaps the normal case for all very old animals. The old, very large individuals, which are to be found in mild winters in Jan.—Febr. and which now only produce very few eggs, have often no spine at all. —

The second pair of antennæ are remarkably long and, with the longest of the

bristles, reach over the hind contours of the valves; the single joints are very broad; this is especially the case with the peduncle which carries the two rami. Highly characteristic is the abdomen; on its posterior edge it has, especially in the male, a very conspicuous excavation; on the posterior side of the excavation the edge carries nine to eleven strong thorns, on the anterior seven to nine, most of them of the same length; the excavation has no thorns or only a few feeble ones. The claws are strongly bent, and provided with two series of well developed thorns, almost reaching each other, in all about fifteen to twenty, and before them a series of very fine hairs. The eye is very large, lying so near the contour of the head that the lenses almost touch it. It is the pigment which is so highly developed. The lenses are few, commonly flattened, lying deeply inbedded in the pigment; the pigment spot is well developed. The ephippium differs in form from our other *Daphnia* species; the dorsal and ventral contour are almost parallel, anteriorly and posteriorly it is provided with long spines which are remains of the contours of the valves which are loosened together with the ephippium and provided with strong thorns. This has already been correctly interpreted and drawn by LILLJEBORG (1900 p. 75 Tab. IX fig. 2) later by v. SCHARFFENBERG (1914 p. 30) who does not seem to know LILLJEBORG'S statement. We have here an apparatus for fixation unknown in most of the other *Daphnia*-species. Along the contours of the valves and spine, upon the antennæ and postabdomen the whole animal is covered with spines and bunches of small bristles, more than any other of our *Daphnia*-species. —

Owing to its globular form, the strongly developed fornices, the peculiar very vigorous postabdomen, its almost total want of any variation combined with locality, season and age, the form of the ephippium, the eye and the high development of spinosity, the species differs strongly from all our other *Daphnia*-species. —

Differing in structure from the other species, *D. magna* also differs very much in life. As mentioned above, its main locality is dirty, very small ponds and pools, often drying up in summer and freezing to the bottom in winter. In ponds of this kind with the bottom covered with fine mud, and often in waterlayers only about 1 dm. deep, the animals are in very close contact with the bottom. We often see the animals resting upon it, mainly sideways but also lying upon the ventral side. The vigorous postabdomen is very similar to that of some of the *Estheridæ*; in this family it is used as a means by which the animal pushes itself forward. I have supposed that *D. magna*, with almost the same structure of the abdomen, the strongly bent claws, the well developed pecten, and the spinosity of the valves, often strongly developed in Cladocera moving in or over mud (*Ilyocryptus*), burrow in mud, quite like the *Estheridæ*. It may be possible that when the water dries up they really do so, awaiting in hollows the time when the pond gets water again. The sudden appearance of large forms from soft mud seems to strengthen this supposition. —

Moving over the bottom they roll over themselves, now and then resting laterally upon one of the valves more rarely upon the dorsal side. When swimming the movements are extremely slow, the antennæ moving, in the old large females, only

about 60—70 times a minute; the movements are mainly vertical, but most so nearest the bottom, and in the aquaria on the opposite side to the light; very often it may also be observed that they follow quite straight horizontal lines with the body lying horizontally in the water. They are hardly ever caught by the surface film.

Regular observations of *D. magna* relating to the propagation have not been carried out. On the other hand, during a long series of years ponds with huge colonies of *D. magna* have often been visited. Combining these observations deriving from all seasons of the year, the following more cursory sketch of the life of the colony may be given.

The drying pools commonly get water in the last part of the autumn or in the beginning of the winter. After severe ice winters there are in early spring only very few just hatched females or none at all in the ponds. During a few weeks the water teems with huge masses, the animals being of very different size. The first hatched reach about 4 mm. and contain one to two hundred eggs. In hot summers and if the water diminishes, ephippial females appear. —

In pools of this nature heavy showers will diminish the formation of ephippia; dry periods will favour it. Of course the downpour has no direct influence upon the formation of the ephippial eggs but in pools which only possess a water layer of a few dcm. and an extension of only about 100 square-m. it is obvious that a heavy shower in an extremely high degree influences all life conditions for the animals; dilution of the water, great differences in temperature, great alteration in the amount of foods, of detritus and in the transparency of the water will occur. In accordance herewith the development of ephippia seems to proceed quite irregularly. Females with ephippia may be extremely common in one sample; 10—14 days later they may be extremely rare. In all samples there are almost always a greater or smaller number of ephippial females present; pronounced sexual periods do not exist.

In permanent pools which have a fairly constant amount of water the whole year, localities which are mainly inhabited by *D. pulex* and not so much by *D. magna*, the sexual periods are more regular with a more conspicuous one in June and another in Sept.—Oct. During the whole summer a greater or smaller amount of females with ephippia may however always occur. After strong sexual periods it may happen, even if the pond has a relatively high water line, that the colony totally disappears, the species lying for months almost only in ephippia at the bottom of the water; this seems especially to be the case with the ponds which possess very abundant water-bloom in the summer months of some years, the surface being covered at the height of the summer with a thick layer of green algæ masses which near the shore pass over into a decaying blue green mass. — When the amount of water bloom mainly deriving from *Clathrocystis* diminishes, *D. magna* appears again. When the water-bloom is not so profuse and the amount of decaying matter is smaller, the animals commonly survive. —

When the temperature falls, a more conspicuous sexual period in October-No-

vember may be the rule. Now it is the temperature of the air which in the first place regulates the life of the colony. If the pond is covered with ice and the ice-bound period is long, the colony will die out, only supporting life in the ephippial stage. On the other hand, if the pond is only icebound now and then for a few days, or open the whole year, the colony holds out; during the months from December to February the number of animals is not so large as in summer, still it is by no means small. In these winter colonies, living for months at temperatures from 0—4° C., as far as my experience goes, we find very few or no ephippial females and no males; the propagation is only parthenogenetic, and almost all individuals may be referred to two sizes: the one extremely large, four to five mm., without spine, often barren, commonly with only a few eggs (5—10) rarely about 40, and another much rarer only about two mm. and mainly without eggs. The first named are the old females which, having produced ephippia in the autumn, are still alive; they now propagate parthenogenetically but with few eggbatches which contain few eggs, and which are only developed very slowly; the last named is the brood deriving from these large females. This brood hardly seems to have begun propagation at these low temperatures. The old females are almost all coated with enormous coverings of algæ and infusoria especially *Vorticellidæ*. Brought into aquaria with large amounts of food and at temperatures 10—12 the brood from the old females develops, but even then this brood uses at all events two to three weeks before it gets eggs; old females brought into the aquaria in December are still living in April, as very large clumsy barren individuals. Their age is at all events about half a year.

Ponds with colonies of *D. magna* differ in autumn from those with colonies of *D. pulex*; these last named ponds almost always, especially in autumn and early spring, possess a brim of ephippia in the watermark line. This is commonly not the case with the *D. magna* ponds. The ephippia of this species are mainly deposited upon the bottom of the ponds and do not rise to the surface, where those of *D. pulex* are caught by the surface film, and later on swept to the borders of the pond by wind and waves. —

V. SCHARFFENBERG has carefully studied the propagation of *D. magna*. If we compare his explorations with the above-mentioned observations, we find great conformity.

V. SCHARFFENBERG (1910 p. 19) states that a female may live in aquaria at all events for 4½ months producing twenty-three eggbatches with 512 individuals; of these individuals 361 are ♀ and 151 ♂; the males arrive quite irregularly, without any connection with the amount of nutriment. He further supposes (1914 p. 4), that the large females may live about one year, hibernating upon the bottom of the water and there producing numerous eggbatches; one of the broods contained 172 eggs. According to my experience the propagation is very much retarded during winter. According to v. S. all females produce parthenogenetic eggs, male eggs as well as females eggs, and also ephippial eggs; the same female may produce a series of

ephippia interrupted by parthenogenetic eggs and, after the production of the ephippia has totally ceased, again develop a series of parthenogenetic broods. The tendency to the formation of ephippial eggs increases with the number of generations; the parthenogenesis is most strongly developed in the first generations. Combining these results with my own observations it seems probable that the great variation in the position of the sexual periods in different years but in the same pond, may be referred to the air temperature in the winter. After winters in which the species has wintered as ephippia the sexual period may begin late; after winters in which the species has wintered as free living organisms, many broods having been developed before the last part of spring, the sexual period will begin very early.

V. SCHARFFENBERG has further shown that in every generation it is possible only by means of alteration in nourishment to produce either parthenogenetic eggs or resting eggs; in the first generation deriving from the ephippia, however, only after a series of broods. On the other hand the sexual differentiation cannot be influenced by means of alteration in external conditions. It is only regulated by means of internal conditions inherent in the organism itself.

WEISMANN has shown that the formation of resting eggs is quite independent of the influence of the male; further that the formation of the ephippia goes on simultaneously with the formation of the resting eggs, and only when the formation of the resting egg has begun. On the other hand the further development of the resting egg is quite dependent upon the impregnation; if this fails to appear the resting egg will not be able to pass over into the broodroom and will be again dissolved in the ovarium.

V. SCHARFFENBERG supposes that it is the penis of the male which opens the way for the egg, whereupon it passes over into the ephippium. Now and then unfertilised eggs may pass over into the ephippium, but they will not be developed. (1914 p. 5.) These views of V. SCHARFFENBERG are, however, strongly combated by OLUFSEN (1918 p. 422).

***Daphnia pulex*. De Geer.**

In my area of exploration *D. pulex* may be found in quite the same duck pools and ditches as *D. magna* and in swarms together with it. The real home of *D. pulex* is not, however, localities of this nature; more often it is to be found in smaller ponds with clear, often peaty water; it is one of the first Crustacea which appears in pit holes, newly dug, and during summer it may often owing to its huge masses colour them red in such localities. It is also the typical representative in many drying up forest pools with the bottom covered with decaying leaves and with peaty, brown water. It occurs here together with mosquito larvæ. In localities of this kind I have never found *D. magna*. Furthermore *D. pulex* is very common in the littoral region of smaller lakes, among the vegetation, and in shallow bays of larger ones.

D. pulex commonly does not reach over 2—2.5—3 mm. rarely 4 mm. Where *D. pulex* and *D. magna* occur simultaneously *D. magna* can be recognised only by its size; furthermore *D. magna* is always much more globular, not laterally so much compressed as *D. pulex* as well as all other species of the genus *Daphnia*. The head is not so much flattened as in *D. magna*, being only rarely $\frac{1}{4}$ of V.¹⁾ The rostrum and the ventral contour of the head differ a little according to the age of the specimen, the number of generations, and the locality. In spring the head is not so much depressed and the ventral contour of the head not so concave as in summer. The spring forms, which are also characterised by their size 3.5—4 m. and their higher number of eggs as well as of abdominal teeth, were regarded as a special form, *D. pennata* P. E. M. — STINGELIN (1897 p. 154) showed that we had to do with a regular seasonal dimorphism and was in this way the first to inaugurate this phenomenon which has occupied so many explores later on. The first pair of antennae are placed wide apart from the apex of the rostrum. Fornices are by no means so strongly developed as in *D. magna*. The length of the spine differs very much, it is longest in the young animals, and in the spring form *pennata*.

During summer colonies are often met with which quite lack the spina (*D. obtusa* Kurz.); the spina is only rarely more than $\frac{1}{3}$ of the length of the valves, in young animals it may reach $\frac{1}{2}$. The second pair of antennae are remarkably short, much shorter than in *D. magna*, commonly not reaching the posterior edge of the valves.

As in all other members of the genus *Daphnia* apart from *D. magna*, the posterior edge of the abdomen has no excavation, but forms a straight line furnished with 12—17 thorns. The claws are not so much bent as in *D. magna*. As well known, *D. pulex* together with *D. magna* belong to those *Daphnia* which possess a so called pecten, two series of thorns or bristles at the base of the claws, the inner consisting of finer the outer of stronger ones; more apically a long series of finer ones which reach near the apex of the claws. In my area of distribution just this character varies a good deal. In many ponds the pecten is very conspicuous, but in others it is absent, in others again rudimentary. As this very pecten is almost the only character by which *D. pulex* may be distinguished from *D. longispina* I have more than once been in doubt as to which of these two species I have had to do with. Regular forthrightly explorations in a pond have shown material which, in one part of the year, mainly contained *Daphnia* with pecten, in another part, a *Daphnia* mainly without pecten or the pecten only slightly developed. The interpretation that we have here two distinct species always succeeding each other is, in my opinion, not always probable.

¹⁾ A. u. T.

T = the total length; H = height; A = the distance from the point of the crista to the centre of the eye; B = the distance from the latter to the valves; V = length of the Valves; S = length of the Spina; A + B = the length of the cara pace; A + B and V are given in the number-columns as fractions.

Already other observers have mentioned the great variation in the occurrence and development of the pecten in one and the same colony, e. g. LILLJEBORG (1900 p. 88), STINGELIN (1897 p. 153), GRESE (1914 p. 4). Furthermore GRESE has shown that of twenty specimens deriving from a mother with typical *pulex* pecten, 12 had a typical *pulex* pecten, 3 an asymmetrical, 1 was typical *longispina*, and 4 were transitional between them both; of twenty-five specimens deriving from a specimen with typical *longispina* claws without pecten twenty four had a typical *pulex* pecten and only one single specimen had an intermediate stage between the two species. The phenomenon, which is most probably much more common than hitherto supposed, is of great theoretical significance. It is just that character which, if the theory relating to the developmental series *D. magna*, *D. pulex*, *D. longispina*, *D. cucullata* were right, must be expected to be subject to fluctuation. That the phenomenon might in some cases be the result of hybridization between *D. pulex* and *longispina*, as WOLTERECK has supposed, (se GRESE 1914 p. 5) cannot be denied. On the other hand it is so widely spread that it is rather difficult to suppose that it could always be interpreted in this way.

The eye is very large but not so large as in *D. magna*, not lying so near the contours of the head as in this species. The lenses are not so deeply indented in the pigment especially not in the summer forms. The pigment spot is well developed. In accordance with the other of our *Daphnia* species, apart from *D. magna*, the ventral contour of the ephippium is not parallel with the dorsal contour, but curved; in our latitudes as well as in all more southern latitudes the ventral edges of the valves are not as in *D. magna* loosened together with the ephippium and used as a means by which the cast-off ephippium is anchored to a subject. Owing to the airspaces in the ephippium it floats on the surface of the water. In late autumn these ephippia often form a broad border near the shoreline; in winter they often form a peculiar ice mosaic, the surface of the ice being covered with thousands of small blackish grey grits. The whole surface of the animal is not so hairy as that of *D. magna*. The development of the cross ridges forming the well known quadrilateral patterns on the valves differs much from locality to locality. It is also dependent upon the age of the animal and whether the animal has produced ephippia or not.

As far as I can see we do not possess a more thorough exploration of the cycle of generations of *D. pulex*, neither from our own latitude nor from more southern ones. This is so much the more regrettable as owing to the excellent explorations of OLUFSEN we possess a series of very thorough observations from Spitsbergen which we are at the present time unable to compare with observations from more southern latitudes.

Unquestionably with regard to its propagation *D. pulex* differs in the different localities to an extremely high degree. On the other hand most of the so-called results of the explorations may be better designated as fugitive impressions which the explorers have gained, than results deriving from regular observations in a series of localities. Observations of this last named kind we especially find in the papers of

MURRAY, LITHINSKY and LIST. The species is regarded both as polycyclic, as dicyclic, and as monocyclic. A series of observations carried on at great intervals have shown (WEISMANN 1876—1879 p. 326) that the species is commonly dicyclic, one sexual period is in May—June and has been several times observed by WEISMANN in natura, the second one not so often; the Dicyclie has also been found by others e. g. STINGELIN (1895 p. 193) in the neighbourhood of Basel.

HARTMANN (1915 p. 441) has observed a colony living in a little pond dug for the purpose; the colony is here dicyclic; the life conditions seem to have been very bad; the main sexual period is in July. JAMES MURRAY (1911 p. 300) has very thoroughly followed a colony of *D. pulex* in a drying up pond. The pond gets water in November and is totally dried up in June. The colony appears in December, it is common in March; in April the males appear. In June the males are very common and simultaneously also the ephippia. Then the pond is dried up and the ephippia lie on the dry bottom till the pond gets water again. The species is pronounced monocyclic. —

In the small ponds of Tatra LITYNSKY (1913 p. 595) has shown that the ponds thaw in May; then the spring generation appears; in the last part of July the males are present; females with ephippia not until August; the sexual period is strongest in September; then many females with empty broodroom appear and these females are to be found the whole winter below the ice. As late as January 10% carry ephippia. The colonies are typically monocyclic with a sexual period in autumn. Also LIST (1911 p. 50) comes to the result that the species is monocyclic.

Other authors again maintain that the species is polycyclic. KEILHACK (1908 p. 21) says: Ephippiumsweibchen und Männchen in fast allen Monaten. — WAGLER (1912 p. 314) comes to the same result: Die Zyklen folgen weiter hin zumal in kleineren Gewässern vielfach so rasch aufeinander . . . daß Ephippien-Weibchen während des Sommers beinahe immer zu finden sind. HEER (1917 p. 45) is of the same opinion. In the months April to November ephippia and males are always present. —

Acyclic colonies have not been found, but it must be added that BANTA (1914 p. 1) has reared a pure line of one hundred generations without sexual forms. The line was propagated by selecting from the first brood of a young female on the day this first brood is released from the brood pouch; there was no evidence of decreasing vigour or loss of vitality in the lines.

In the alpine region the authors come to quite different results. ZSCHOKKE (1900 p. 175) says that it is poly- or dicyclic, KLAUSENER (1908 p. 407) for the "Blutseen" that it is monocyclic; in the arctic *D. pulex* as well as all other Cladocera seem to be monocyclic (W-L. 1894 p. 144; HABERBOSCH 1920 p. 54).

With regard to hibernating below the ice most of the authors from Central-Europe maintain that the colonies die out entirely in winter, and that the species only hibernates as eggs in the ephippia (STINGELIN 1895 p. 194, and this is in accordance with the experimental studies of OSTWALD (1904 p. 34), who points

out that at a temperature of 0—5° the females always die out in the course of 1—3 days. — Only LIST (1911 p. 50) has observed *D. pulex* free-living below the ice.

In Sweden LILLJEBORG (1900 p. 93) has observed *D. pulex* in Decbr.—January “unter dickem Eis, wenn dieser nur nicht den Boden erreichte”.

For my own part I have followed a *D. pulex* colony in a pond which got water (originally as snow) in the middle of April and was quite dry in the first part of June. Furthermore in the years 1916—1919 the plancton was studied in nine different ponds, all being from much below up to about 1 ha. The exploration was carried on every fortnight; most of the ponds had peaty water; some of them were covered in summer with a rich vegetation, some had a central part free surrounded by a broad girdle of *Potamogeton natans*. From duckponds etc., the real home of *D. magna*, no regular observations have been carried on with regard to *D. pulex*; but very many from different ponds of this nature irregularly dispersed over a long series of years at different times of the year.

Beginning with these last-named duckponds I cannot deny the possibility of *D. pulex* being really polycyclic in localities of this kind; at all events, in the time from May to Decbr., females with ephippia and males have been found at all times. The assertion of KEILHACK and of WAGLER relating to polycyclic may perhaps hold good; however, according to my experience, only for localities of this kind. — From one of these ponds I got a sample in the last part of Decbr.; the pond was half icecovered. The water teemed with *D. pulex* but no female had ephippia; many were empty, others had two eggs in the brood-room. —

In ponds which are all extremely small hollows with water only in spring, either such as have grassy bottoms, lying in open plains, or in the wood, with the bottom covered with decaying leaves, localities which commonly all dry up in June, and are filled with snow and snowwater in December, *D. pulex* appears about one or two weeks after the ice has melted. Commonly the whole cyclus does not last more than six to eight weeks. In these weeks the water is filled with enormous quantities of parthenogenetic females; the water is often red. Then suddenly, often in the course of only a week, in the beginning of June almost all the females carry ephippia; these are thrown off, and in many years the ponds dry up a week or two later. In localities of this kind the species is mainly monocyclic. In very wet summers many of these hollows possess water the whole year round or are filled again in July. In the first case *D. pulex* will be dicyclic with a pronounced sexual period in June and another in autumn. In the last case most of the observations seem to show that the brood from the ephippia is not hatched and that the brood does not appear before spring.

The above-named remarks are based upon numerous observations from the years 1917—1920 in which material for my work, *Contributions to the Biology of the Culicidae* was brought together. Almost all these ponds harboured *D. pulex*; many of them were visited regularly; the Daphnids were caught together with

the mosquito larvæ; and with a lens it was observed if the swarms had ephippia or not. —

The main result is that in dry summers *D. pulex* is monocyclic in localities of this kind and may be dicyclic in wet, further that new filling of a locality which has been laid totally dry is commonly not enough to break the resting period of the egg. —

In ponds which never dry up but may freeze to the bottom in cold winters, which have a free "pelagic" region and the bottom covered with a layer of *Zygnemaceæ* or *Oscillatoria* which in warm periods are lifted to the surface, the cycle of the colony differs from the above-named.

From a pond of this kind, Nøddebo pond, which is only about 150 m. in circuit, regular explorations have been carried on every 10th day from 1922 to 1925. In the winter 1923—1924 it was frozen over and unquestionably to the bottom for about 140 days; on the other hand during the winter 1924—1925 it was practically open, being during the whole time only covered with thin ice a few days in Dcbr. 1924 and for 10—12 days in March.

The pecten in the colony is often badly developed, in some samples very pronounced; now and then intermittent stages occur. Nevertheless I suppose it most correct to refer it to *D. pulex*, but I confess that many specimens are typical *D. longispina*. To regard the colony as consisting of two well defined species *D. pulex* and *D. longispina* presents biological difficulties of different kinds.

During the spring of 1922 the species was remarkably rare; as late as $^{16}/_{VII}$ the number was but small. From the last part of July to the last part of September the water teemed with specimens. The propagation was very lively, but no males or ephippia appeared. The tp. of the water was from 0 to 3° C. The first ephippia were seen on $^{25}/_{IX}$, the sexual period lasted the whole of November. From $^{1}/_{XI}$ to $^{17}/_{XII}$ the pond was three times frozen over and three times again thawed. On $^{1}/_{I}$ 23 the pond was again ice covered but free again by $^{1}/_{II}$. A sample was taken on $^{4}/_{II}$ 23 when the pond was for a short time ice free, but no specimens were seen. It was again frozen over and finally thawed on $^{15}/_{III}$. By $^{10}/_{IV}$ a few very large females which may perhaps have wintered were found; the number of eggs was very large about fifty. During the time May— $^{15}/_{IX}$ the species propagated only parthenogenetically; the number of eggs was great in spring but relatively small in July, being only 4—6. Then in the last part of July and during most of August the number of eggs rose to twenty or more. In September it sank again and by $^{20}/_{IX}$ the first ephippia were seen. The sexual period lasted the whole of the autumn and still when the pond was icebound by $^{24}/_{XI}$ 23. During the long period from $^{24}/_{XI}$ to $^{20}/_{IV}$ 24 the pond was covered with ice. From $^{20}/_{IV}$ till $^{15}/_{V}$ four samples did not give one single *Daphnia*, on $^{24}/_{V}$ young brood appeared, on $^{31}/_{V}$ they began to produce eggs and on $^{4}/_{VI}$ the propagation was lively. Again the parthenogenetic propagation lasted during the whole of the summer from the last part of May to the middle of September. On $^{3}/_{VIII}$ a few ephippial females were found; the num-

ber of eggs was but small during the whole period, and the species not so common as in 1923. Then in September the sexual period began, but it was but slightly pronounced. From the last part of November 1924 and during the whole of the winter when the pond was open parthenogenetic females were present, but only in a few specimens, and the number of eggs was but small. The exploration clearly shows that we have to do with a pronounced monocyclic colony, which during three years had only one sexual period yearly which in all the three years was in Sept.—Nov. It seems as if the severe winter in 1923—1924 in which the pond was frozen to the bottom in some degree weakened the colony.

Most probably the result of the exploration of this pond may almost be regarded as a paradigm for *D. pulex* in ponds of this nature; at all events it is highly remarkable, that in the numerous localities of this nature pronounced sexual periods are only rarely met with in the time May—Sept., everywhere the propagation is mainly parthenogenetic during this time. — In the above-named larger ponds with a central part free from vegetation in which samples were taken every fortnight in 1897—1900, *D. pulex* is really present, but strangely enough never as a plancton organism and never in the central part of the ponds. If Daphnids are present, they are represented by *D. longispina* and *Ceriodaphnia* species. *D. pulex* is here living in the Potamogeton region but is by no means so common as *Simocephalus*, *Eurycerus* and other *Lynceidae*. In these larger ponds *D. pulex* is a pronounced littoral species, and is present here the whole year from May till the ponds are ice covered. In localities of this kind where the vegetation is very rich, and where the species lives together with many hundreds of different organisms, it is very difficult to point out the max. and min., most probably the amount of specimens is not subject to great variation. As, however, the ehippia have never been found on the surface during summer whereas, together with ehippia of *Simocephalus* and *Ceriodaphnia*, they form whitish grey lines in late autumn on the decaying vegetation in the water rim, I regarded it as highly improbable that sexual propagation should play a more prominent part before September—October. The following observations seem to corroborate this view.

From one of the ponds Fortundam about 1—2 ha large, free from vegetation in spring but in later summer and autumn covered with a thick carpet of *Potamogeton natans*, a series of samples from $\frac{9}{IV}$ to $\frac{3}{VIII}$ and then again from $\frac{4}{IX}$ to $\frac{27}{XI}$, were taken every ten days. No specimens were found before $\frac{6}{V}$. From the last part of May to $\frac{10}{VII}$ *D. pulex* had an enormous maximum in the pond. Nevertheless not a single specimen with ehippia was found; the propagation was practically only parthenogenetic; in the last part of June *Volvox* had an enormous maximum, giving place in the last part of July to *Ceratium hirundinella*; the first-named species colours the water green, the last-named which has its max. as late as $\frac{3}{VIII}$ makes the water yellowish green. During these two enormous maxima the number of *Daphnia* seemed to diminish. By $\frac{11}{IX}$, when the *Ceratium* max. disappeared, *D. pulex* appeared, again in enormous quantities. Now, however, almost all

females carried ephippia. In spring the size was much greater and differed very much in every sample; now all were almost of the same size; there was but little brood and the size was relatively small, the length being only about 2 mm. The diminution in size during summer and the fact that the ephippial females are rather small is corroborated by other observers e. g. HARTMANN (1915 p. 446). PAPANICOLOU (1910 p. 749) has observed that this is due to the fact that the ephippial females grow slower, that they are ripe later than the parthenogenetic ones, and that there is a greater interval between the moults. It seems that he supposes that the ephippial female is a special form differing from the parthenogenetic. This is most probably not right; nevertheless his observations can very well be used; they must only be interpreted in another manner. In the last part of October the sexual period ceased. In the course of a fortnight the water layers were so to speak emptied of *Daphnia*, and the surface of the water in all small bays was covered with a thick coherent layer of ephippia. The colony in the pond is pronouncedly monocyclic.

Comparing the results with those of KEILHACK and WAGLER who both maintain that *D. pulex* in their district of exploration is polycyclic, and that every generation and brood is able to produce ephippia, it is evident that the difference is very conspicuous. Especially in duckponds *D. pulex* may be polycyclic but in all other hitherto explored localities the species has always had pronounced sexual periods, very rarely two, almost always only one single sexual period, always in Sept.—October. Neither KEILHACK nor WAGLER have published the results upon which they base their supposition. They are also opposed to the views of WEISMANN who commonly finds two sexual periods, a shorter one in spring, and a much longer one in autumn. —

D. pulex may or may not hibernate under the ice as a free-swimming organism; this depends in the first place upon the tp. of the air. If the ponds freeze to the bottom all free living individuals are killed and all specimens appearing in May derive from ephippia, then the specimens are all of the same size. In mild winters *D. pulex* may also hibernate as a free-swimming organism; the number is commonly but small; ephippia are not developed; the parthenogenetic propagation is but small and is not great enough to keep up the same number as in December. When April—May arrives the ephippia are hatched. The waters teem with young brood, but in the swarms we find some very large females 2.5—3 mm. These females produce very large egg batches often up to 50 eggs or more. They may still live in the last part of May and are then often empty; they have then commonly reached a size of about 4 mm. Immediately before they are getting empty they may in some ponds produce ephippia. I have seen no males; the ephippia have a peculiar appearance; they are of a homogeneous blackish brown colour; the egg-lodges are not elevated and not marked off as whitish spots, the two eggs lie orientated in all directions in the ephippium, not perpendicularly on the long axis; most probably they will not develop.

The number of free-swimming individuals under the ice during winter differs

from pond to pond and from year to year; their number is always small in early spring and then they may always be recognised owing to their size. —

The most thorough observations carried on upon *D. pulex* we owe to OLUFSEN (1918 p. 392). He has explored the life conditions of the species in numerous localities on Spitzbergen.

In the following I will compare his results with those from my own and from more southern countries. His explorations first show that the size in the arctic races is smaller than in the more southern ones; the size is commonly only 2.3—2.4. The greatest size is 3.3, without spina. The size increases from brood to brood; the last broods of the first generation are larger than the first; further the second generation is smaller than the first; the phenomena are due to want of food and early evaporation of the water; this again has provoked propagation at an early stage of the life of the animals. —

The local variations are but small; it seems that the races are all provided with typical pecten upon the claws. Temporal variation manifests itself with regard to the length of the spina. OLUFSEN maintains that the length of the spina varies regularly in accordance with the temperature; the higher the temperature is, the longer is the spina. The specimens deriving from the ephippia have a short spina. As the temperature rises the spina gets longer in the succeeding broods. When the temperature sinks the broods get a shorter spina from birth. One and the same individual gets no longer spina because the tp. is increased but at sinking temperatures the spina shortens uninterruptedly. Neither nourishment, nor number of generations, nor inner conditions have any influence upon the length of the spina. The length of the spina is determined during the embryonal development. There is no præinduction; the shortening of the spina in ripe individuals is due to the direct influence of outer conditions. According to OLUFSEN this temporal variation is due to efforts to augment the floating power of the young Daphnids with small power of locomotion; in the older and larger individuals with stronger locomotion the spina has no significance at all, and is reduced. At the present moment we lack material to compare these phenomena of the Spitzbergen Daphnids with those of more southern countries. With regard to the propagation OLUFSEN arrives at very noticeable results.

His main result is that the Spitzbergen races only propagate parthenogenetically and that ephippial eggs are unfertilised eggs; in the enormous material of animals and observations OLUFSEN has never seen a male; he correctly states that males are never found in the arctic; on the other hand ephippial eggs play a greater part in the arctic cycles than in the more southern ones. The form of propagation for the Spitzbergen Daphnids is an asexual or parthenogenetic monocycle, an alternation between the subitane eggs and resting eggs all produced parthenogenetically. OLUFSEN further maintains that this peculiar form of propagation is a necessity of life under arctic conditions; the period of vegetation lasts only two months; life during winter is an impossibility whilst the small ponds all freeze to the bottom,

and even the period of vegetation is often restricted owing to evaporation of the water. From a long series of very thorough explorations OLUFSEN is able to show that the production of resting eggs sets in in every part of the cyclus even in the first brood of the ephippialfemales; upon this point the Spitzbergen races differ conspicuously from what is customary under more southern conditions. The formation of resting eggs depends in the first place upon the intensity of assimilation, and this is again dependent upon the evaporation of the water in the locality in question. —

At the present moment it is rather difficult to take decided ground upon the subject of these highly remarkable results which differ from all those of more southern localities, and which so to speak reverse most of what we consider correct with regard to the propagation of the Daphnids.

At a first glance it seems highly peculiar that an organism should, over a great part of its area of distribution, be able always to propagate parthenogenetically; on the other hand it must be remembered that organisms which are able to propagate as well sexual as asexually or parthenogenetically and which have a regular change in the two sorts of propagation, seems to maintain the locality under more northern or arctic conditions owing to this very asexual or parthenogenetic propagation, and that the use of the sexual propagation is augmented the further south the colonies live. As far as we know this is the case with *Bryozoa*, *Planaria*, *Ostracoda*, *Hydra* and especially with many *Phanerogams*. Further on it may be remembered that v. SCHARFFENBERG (1910 p. 1, 1914 p. 5) has shown that ephippia are formed without fertilisation; he has also seen that eggs in females which are not fertilised have been deposited in the ephippia. LITYNSKI (1913 p. 592) has also observed that unfertilised females produce ephippia. Both authors, however, maintain that these eggs cannot be developed. The new fact which OLUFSEN has pointed out is that the development of ephippial eggs without fertilisation in the Spitzbergen Daphnids is no pathological phenomenon but a quite regular one. If this is true, amphimixis cannot be regarded as causing the conformity of the arctic colonies of *Daphnia*, and some main points with regard to the main causes of the temporal variations must be altered. To this point we shall return later on. It will now be tried in our laboratory to force our own *D. pulex* to produce ephippia and resting eggs without impregnation and make these eggs develop; the first part may be regarded as highly probable; if the second part is possible is questionable.

It is of great interest that OLUFSEN has been able to determine if a *Daphnia* has produced ephippia owing to variations in the spinosity of the dorsal contours, and that the ventral edge of the valves remains upon the ephippia when the ephippia are thrown off, quite as in *D. magna*, a phenomenon which is quite unknown in *D. pulex* in more southern races. OLUFSEN's supposition that these spiny strings are intended to anchor the ephippia during inundation to that low watermark line on which they are deposited so that they are not swept away into dry localities, seems

highly probable. The number of subitan eggs found by OLUFSEN is smaller than in more southern localities. There are in Spitsbergen only three generations; the first generation is commonly the only one which gets time to produce subitan eggs; the greatest number is 36, commonly it is much lower; if the second generation forms subitan eggs the number is not more than 5 to 8. The third does not generally reach maturity. My own old observations (1894 p. 141) relating to the number of eggs in the brood room of the *Daphnia* from Greenland, and which all indicate a too low number of eggs, have been carried on upon old alcohol material; unquestionably the eggs and broods have often dropped out of the brood room; too low a number is therefore given. In this connection it is of interest that the explorations of HABERBOSCH in Greenland (1920 p. 54) have given results very similar to those of OLUFSEN; he has, however, observed males, but they are extremely rare.

It may still be added that from other countries we have often during the last few years become acquainted with *Daphnia* species which live a real planctonic life in larger lakes, and nevertheless are furnished with a conspicuous pecten upon the claws. This is of interest if we remember that in very small ponds with a depth of only a few dcm. we may find Daphnids which have no pecten and nevertheless most probably may be referred to *D. pulex*. Planctonic races of *D. pulex* have first been described by FORBES (1893 p. 242) and later by BIRGE (1892—1893) from Madison lake. In Europe BURCKHARDT (1900 p. 448) has found a *D. pulex* de Geer nov. var *pulicarioides* Burck. in the lake of Lugano; this has been found again by STEINER (1913 p. 93). it is indicated as a summer form. Later on BURCKHARDT (1914 p. 6) says that it is absent in April and rare in October. In 1913 LITYNSKI (p. 587) has described another pelagic *Daphnia* with pecten from the Tatra lakes (*D. Wierzejski*); he supposes that it is identical with *D. pennata* O.F.M. which STINGELIN (1895 p. 195) has supposed was the springform of *D. pulex*. The species is monocyclic with lively parthenogenetic propagation in summer, and a sexual period in autumn. The species lives the whole winter below the ice. The swarms are then found partly by the old females which have now thrown off their ephippia and are barren, and partly by young females which have no eggs in the brood room and begin parthenogenetic formation in spring.

In the same category most probably belongs *D. Zschokkei*, described by STINGELIN (1894 p. 378) and the variety *vigezzina* MONTI. — Also WAGLER (1912 p. 356) has found a similar form near Leipzig which with regard to its pecten stands nearest to *D. longispina*. »Sonst weiss sie alle durch das Littoral induzierten Eigenschaften auf, in dessen Nähe sie gefischt wurde.«

D. longispina.

With regard to the very difficult systematics of the group *D. longispina* — *D. cucullata* I have followed WAGLER (1912 p. 332) who in my opinion at our present stage of knowledge has come as near as possible to the truth. I only fear that the

time will soon come when it will be impossible any longer to distinguish strictly between the two species *D. pulex* and *D. longispina*. —

WAGLER has divided *D. longispina* into two subspecies: *D. longispina* and *D. hyalina*. Of these two subspecies I suppose that *D. hyalina* is rare in our country; it has only been found as a plancton organism in two of our lakes, the lake of Sorø and the lake of Tjustrup. It was found there by P. E. MÜLLER (1868 p. 116) and described as a new species *D. pellucida*. Later on (1870 p. 6) he referred it to *D. hyalina*, and SARS (1890 p. 10) and LILLJEBORG (1900 p. 101) have followed him on this point. — It has never been found in smaller ponds. The subsp. *D. hyalina* may best be distinguished from subsp. *D. longispina* by its high hyalinity and its small eye with well developed crystal lenses; the rostrum is extremely acute and appressed to the valves; the ventral contour of the head is straight; the spine is as in *longispina*, long, but commonly bent upward. WAGLER maintains that also *hyalina* may pass a Cyclomorphose and in summer be provided with a galea. In our country this has not been observed. It is commonly regarded as monocyclic (SCHNEIDER 1913 p. 212).

D. longispina forma *longispina*.

WAGLER and others maintain that in their area of exploration very many extremely small watermasses, even duckponds, may be inhabited by *D. longispina*, especially, as far as I understand, in the form *D. longispina longispina*. Also HARTMAN (1915 p. 439) at Graz seems to have arrived at a similar result. His explorations derive from a little pond only 40 m. long, 20 m. broad and 1 m. deep. In the Alps as well as in Central Europe and high up in Sweden (EKMAN 1904 p. 122) *D. longispina* is well known as a pronounced inhabitant of small even drying up pools, whereas, curiously enough, *D. pulex* seems to be the only representation in the far North as well as in Greenland (HABERBOSCH 1920 p. 34) and upon Spitzbergen (OLUFSEN 1918 p. 392), *D. longispina* being totally lacking. In Finland LEVANDER (1900 p. 67) has shown that in the small water masses on the skerries either *D. pulex* or *D. longispina* may occur. Only for a short time and exceptionally they may occur simultaneously. Already HABERBOSCH (1920 p. 34) has paid attention to their particular distribution. SCHEFFELT (1909 p. 110) says as follows: "Die Muttertiere begeben sich (!) wohl aus Nahrungsmangel in littorale Region wo dann besonders im Monat Januar die Ablage der Ehippien stattfindet". This is not correct. The ehippial females throw off their ehippia in the pelagic region. The ehippia, as soon as they are loosened from the animals, owing to their amount of air will ascend to the surface from which the winds blow them into the littoral region.

In my own area of exploration *D. longispina longispina* has been found as well in very small ponds with peaty water, as in Cyanophycé ponds and in the pelagic region of our largest lakes. I have been inclined to refer most of the red clumsy Daphnids with a pecten more or less conspicuous, and which live in very

small water masses, often in volume of a few hundred cubic meters, to *D. pulex*. It is possible that others will arrive at another result and e. g. refer *D. pulex* from Nøddebopond to *D. longispina*. In localities of this kind it is rather probable that in our latitudes the transformation of *D. pulex* into *D. longispina* is only taking place in our day; that this transformation is more pronounced in one pond than in another; and that in the same pond in one year the main part of the specimens may be most nearly related to *D. pulex*, in another to *D. longispina*. It is a matter of taste how the colonies should be determined. It may be added that the colonies seem to be mainly monocyclic but may also be dicyclic. Polycyclic colonies I have hitherto never found in this species. Strangely enough, in Central Europe polycyclic colonies have fairly often been observed, especially by WAGLER (1912 p. 348 and 315); see also KEILHACK (1909a p. 22). WAGLER has often observed dicyclic colonies and very thoroughly studied the polycyclic colonies in small ponds near Leipzig. His observations seem to show that the old females, having thrown off their ephippia, again begin parthenogenetic propagation, and that the ephippia which have been thrown off are hatched during the same summer in which they are found. In September—October begins the long sexual period before winter whereupon the colony dies out. These colonies are said during the time $^{11}/_V$ to $^7/_IX$ to possess 4 sexual periods. In our country we have never seen anything of that kind. The colonies of the Cladocera in the far North are always monocyclic; it is possible that when polycyclic cannot be observed with us, it is the climatic conditions which already here begin to assert themselves.

At page 17 it has been pointed out, that *D. pulex* when it occurred in larger ponds, was always a pronounced littoral form here which has not hitherto been found in the central part of the pond, rarely in the Potamogeton region, and numerous only very near the shore. Just the central part of these ponds is the real home of the typical *D. longispina* where it often lives together with species of *Ceriodaphnia* commonly *C. pulchella*. In larger ponds with peaty water the species is rather hyaline in spring, in autumn, often red. The head has no galea. $\frac{A+B}{V} = 1/4$. The contours of the head are round, the ventral contour is more or less concave, most concave in autumn; the eye is of middle size, the rostrum is rather acute, not appressed to the valves, the spina is long, commonly half the length of the valves; there is often no conspicuous pecten, the claws are often almost typical *longispina* claws. A temporal variation does not exist, at all events it is extremely small and is restricted to a mere concavity of the ventral contour of the head in autumn, and a little higher crista during summer. The pond races which WAGLER (1912 p. 351) describes show most of the same structures. The eye is a little larger and the spina perhaps a little shorter than in spring. The size is about 1.9 to 2.3 mm. It is largest in spring. In some ponds, and this may be the rule, the species totally disappears during winter; it seems to arrive in the pelagic region rather late, not before June, when the temperature of the water is between 16—18° C. In a few

ponds a few ehippial females have been found in the last part of June but no males. During summer the watermasses are filled with enormous quantities of *Daphnia* material; the swarms have then a very conform appearance; huge maxima may occur in July—August but commonly not before September. In October the males are present in great numbers and most of the females carry ehippia. It is, as far as I have hitherto found, pronouncedly monocyclic.

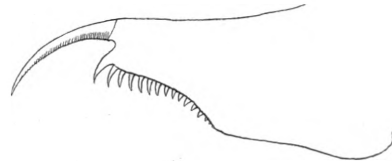
D. longispina in Klarelake.

Tab. I.

Dato	T	A	B	A + B	V	$\frac{A+B}{V}$	S	H	eggs	Nr.
¹³ / ₅	2100	168	252	420	1630	⁴²⁰ / ₁₆₈₀	840	1512	20	1 a
—	1008	84	168	252	756	²⁵² / ₇₅₆	588	588	Ehipp.	1 b
—	1008	84	168	252	756	²⁵² / ₇₅₆	588	588	2	1 c
¹⁰ / ₆	1680	84	252	336	1344	³³⁶ / ₁₃₄₄	504	1092	6	2 a
—	1294	118	168	286	1008	²⁸⁶ / ₁₀₀₈	420	622	0	2 b
²⁴ / ₆	2436	134	202	336	2100	³³⁶ / ₂₁₀₀	588	1680	20	3 a
—	1680	84	252	336	1344	³³⁶ / ₁₃₄₄	504	1092	Ehipp.	3 b
—	1126	118	168	286	840	²⁸⁶ / ₈₄₀	336	672	—	3 c
—	1092	84	168	252	840	²⁵² / ₈₄₀	336	672	0	3 d
—	672	67	101	168	504	¹⁶⁸ / ₅₀₄	336	336	0	3 e
²¹ / ₇	1092	84	168	252	840	²⁵² / ₈₄₀	336	672	0	4 a
¹⁴ / ₉	1260	84	168	252	1008	²⁵² / ₁₀₀₈	504	756	5	5 a
—	1008	84	168	252	756	²⁵² / ₇₅₆	504	504	2	5 b
—	554	50	84	134	420	¹³⁴ / ₄₂₀	252	236	0	5 c
⁵ / ₁₀	1092	84	168	252	840	²⁵² / ₈₄₀	336	672	2 Ehipp.	6 a
—	370	118	168	286	84	²⁸⁶ / ₈₄	252	672		

In one of these ponds, Klarelake, near Hellebæk, North Seeland, with very peaty water, with a depth of about 2 m., little vegetation and a large "pelagic" region, a very particular race of *longispina* was found which has troubled me very much, especially because I have been unable to study it regularly from the boat. Samples have only been taken from ¹³/_V, ¹⁰/_{VI}, ²⁴/_{VI}, ²¹/_{VII}, ⁷/_{VIII}, ¹⁴/_{IX}, ⁵/_X 1924; only the samples ²⁴/_{VI}, ¹⁴/_{IX} and ¹⁵/_X have been taken from the boat. In the sample from ¹³/_V a *D. longispina* was found which appeared in the sample in two different sizes, the one (fig. 1 a) was very large, T 2100 with A + B only ¹/₄ V, and A only about 160. The form was extremely clumsy, the height being 15—1600. The eye was very large; the head had a peculiar resemblance to that of *D. magna*. The spine was straight, rather long, about 800. The form was only found in a small number. The number of eggs was about 20. Together with this form was found another more common one, the size of which was always about 1000, A + B was about ¹/₃ V and A only about 80. The height was normal, about 550—600. This form had commonly two eggs, never more; some were empty and seemed hitherto not to have produced eggs; some of them carried ehippia. The facts could best be interpreted so, that the large females were the wintering generation, which had now produced the smaller ones which had just begun the egg production, and of which

some of the first broods had curiously enough already now produced ephippia. The sample $^{10}/_{VI}$ was also taken only from the shore. The result was almost the same; large females with a high number of eggs and a smaller size with $T = 10-1200$ either without eggs or only two; a few carried ephippia. By $^{24}/_{VI}$ a boat was used. The net was first drawn through the whole length of the lake, later on at three transversal lines, partly at the surface, partly at the bottom; in all these large samples only very few Daphnids were seen. Finally in the middle of the lake, at the deepest spot, the net was drawn round in a circle. To my great astonishment the net contained enormous quantities of red Daphnids and many *Holopedium*. It seemed as if almost all the *D. longispina* material of the lake was standing in a very thick and strongly limited swarm in the deepest part near the bottom. It was bright sunshine. A more thorough examination of the swarm showed that in it there lived a rather restricted number of very large and extremely clumsy forms. The T was 2.4 to 2.8 (Fig. 3 a); most probably they are among the largest *D. longispina*-forms hitherto found; this will especially hold good if we remember that V is 2100 and that $A + B$ may be only about $^{1}/_{4}-^{1}/_{5} V$, shorter than even in *D. magna*. A is only 134. The height is 17-1800; the spina is short about 600, straight. The number of eggs is 20-30. The form is further characterised by its extremely short antennæ, these reaching only a little over the



D. longispina Klarelake.
Abdomen. 80×

middle of the valves; the swimming bristles especially are extremely short. Most peculiar is also the tail; many of the females show on the posterior edge a slight excavation quite as in *D. magna*; the post-abdominal thorns are remarkably strong and present in a number of 14-16; the claws are more strongly curved than is commonly the case with those of *D. longispina*; there is no pecten. These large females have produced the enormous swarm in which they lived. This swarm consisted of enormous quantities of young brood (fig. 3 e) and of animals of the size 11-1200 with $A + B$ always a little $< ^{1}/_{3} V$ (the primiparæ). The peculiar thing now was, that among these millions of individuals there was not a single one with parthenogenetic eggs; on the other hand there were very many females with ephippia, and almost always in the size 11-1200; in most of them ephippia were not fully developed; simultaneously there were extremely many males; the males were almost as numerous as the females, of the size 11-1200. — Between this size 11-1200 and the large ones of 25-2700 there were a few intermediate stages of 16-1700, but never more; some of these carried ephippia but always of a homogeneous brown colour, without white egg lodges; most of them had 4-6 eggs. — It seemed as if the swarm formation was connected with the sexual propagation; enormous masses of males and females which all unquestionably originated from the large females were pressed together in a very small space; these young females all seemed to produce ephippia perhaps in their first brood. During the time $^{24}/_{VI}$ to $^{14}/_{IX}$ I have

two samples from $^{21}/_{VII}$ and $^{7}/_{VIII}$, both taken from shore; as the net, however, reached almost to the middle of the lake and was drawn in near the bottom, the sample may be regarded as rather reliable. It seems as if the species almost disappears from the lake. It was rare by $^{21}/_{VII}$, present only in the size 11—1200 but empty without eggs and no ephippia; by $^{7}/_{VIII}$ only a single specimen was found; it seems, as if the whole colony were now only present as ephippia. By $^{14}/_{IX}$, when a boat could again be used, very many and very large samples were taken. At the bottom as everywhere the species only occurred in the size of 11—1200; it was remarkably rare, but the parthenogenetic propagation was now going on; a few females carried 5 eggs, but most of them, the size of which was only 1000 (5 b), had only two eggs and many none; no ephippial eggs and no males were found. By $^{5}/_{X}$, when the boat was again used, the number had increased; females of the size 1000—1100 were now fairly numerous, now producing two eggs and some of them ephippia; a few males were found. By $^{15}/_{XI}$ a sample taken from shore contained only a few females of the size 10—1200, producing two parthenogenetic eggs.

Even if many more samples would have been desirable, it seems rather certain that the species in Klarelake is really dicyclic. The colony is further characteristic by the fact that the wintering females reach such an enormous size and fertility, but especially because it seems that the first generation produced, deriving from those females, dying out in June, most probably before any parthenogenetic propagation, pass directly over into a sexual period and produce ephippia. On the other hand it may be possible that there has been one parthenogenetic generation, but it is not very probable, because all females of the size 1000 are empty. The large wintering females may, shortly before they die out, produce enormous quantities of males. After June there is one of two possibilities. One is that the species practically dies out during summer and the ephippia produced in June are hatched in September, a new sexual period setting in in October; the few wintering females grow in spring to enormous size and fertility and a new generation begins. The other is that the ephippia produced in June are not hatched before next year, and that a slight number of parthenogenetic females survive the summer and begin sexual propagation in autumn.

Apart from ponds with peaty water *D. longispina* may also be found in typical Cyanophycé ponds in such were the water is almost always overfilled with Phytoplankton which gives it its colour; in summer the surface is covered with a thick layer of Cyanohycea; the temperature is very high. We have here to do with localities where races of *D. longispina* and *D. cucullata* meet each other. These races are not common in our country; only relatively few Cyanophycé ponds possess them and the maxima they reach here are commonly but small. In many samples in the summer half of the year they can only be observed in small number. —

In the *longispina* races from ponds of this nature we do not find the homogeneous stamp which characterises the races from ponds with peaty water. —

In one pond of this nature, the Hestesko pond in the Royal park at Frederiks-

D. longispina. Hestesko pond.

Tab. I.

Dato	T	A	B	A + B	V	$\frac{A+B}{V}$	S	H	eggs	Fig.
1924	$17/6$	1126	118	168	286	$840/286$	286	672		1
	$30/6$	2016	168	336	504	$1512/504$	420	1176	7-10	2
	$15/7$	1226	84	302	386	$840/386$	504	840	7-10	3
	$15/8$	1395	101	286	387	$1008/387$	588	672	7-10	4
	$31/8$	1646	134	336	470	$1176/470$	672	984	7-10	5
	$10/9$	1445	101	336	437	$1008/437$	672	984	5-7	6
	$29/9$	1378	118	252	370	$1008/370$	672	588	5-7	7
	$15/10$	1361	101	252	353	$1008/353$	756	588	6-8	8
	$25/10$	1814	134	420	554	$1260/554$	504	1008	Ehip.	9
	$11/11$	1445	101	168	269	$1176/269$	672	984	6-8 eggs	10
	$28/11$	1630	118	336	454	$1176/454$	336	1512	28	11
	$8/12$	1613	101	336	437	$1176/437$	504	840	Ehip.	12
	$28/12$	1613	101	336	437	$1176/437$	504	840		13
1925	$18/1$	1932	252	336	588	$1344/588$	420	1092	6	14 a
	$18/1$	1394	134	252	386	$1008/386$	420	840	0	14 b
	$20/1$	1730	134	252	386	$1344/386$	420	1092	5	15
	$16/2$	1562	134	84	218	$1344/218$	420	1092	7	16
	$16/2$	722	84	134	218	$504/218$	420	420	0	17
	$2/3$	1730	134	252	386	$1344/386$	420	1092	11	18
	$30/3$	1092	84	168	252	$840/252$	588		0	19
	$11/4$	1260	84	252	336	$924/336$	504	756	0	20
	$28/4$	2100	168	252	420	$1680/420$	588	1260	30-35	21
	$15/5$	2722	168	370	538	$2184/538$	672	1680	35	22
	$15/5$	1764	168	252	420	$1344/420$	588	1260	20	23
	$15/5$	1260	84	252	336	$924/336$	672	672	6	24
	$26/5$	2016	168	336	504	$1512/504$	504	1176	4-9	25
	$26/5$	1092	84	168	252	$840/252$	420	588	2	26
	$26/5$	1210	84	202	286	$924/286$	420	672	Ehip.	27

borg, *D. longispina* was found and then studied regularly from $7/IV$ 1924 to $1/VII$ 1925. During the time when the pond was open there was never more than about 10 days between the samples; only from $15/VII$ to $15/VIII$ 1924 there were no samples. The pond was ice-covered from $1/XII$ 23 to $19/IV$ 24, in all 140 days. The pond was half open by $7/IV$; in the sample no *Daphnia* could be found. In all the samples till $17/VI$ no *Daphnia* appeared. By $17/VI$ the ephippia must have been hatched and the first young animals ($T = c. 1100$) appeared in the plancton. By $30/VI$ (Fig. 2) the size had increased much ($T = 2600$) and the large females carried about 30 eggs. In the rest of June and almost the whole of July the number was but small. In the last part of July the number increased and the number of eggs is often 6 to 8. From $1/VIII$ a maximum began. The number of eggs is the same. In the last part of August and to the middle of November the number of specimens steadily increased; the number of eggs was always the same, 4-6, never more. By $29/IX$ the first ephippia and a very few males appeared. The number of females with ephippia was much increased by $15/X$; the same was the case on $25/X$ (Fig. 9) when

simultaneously very many males were present. At this moment the sexual period was at its highest. Already by $1/XI$ the number of males decreased and there were many females which had thrown off their ephippia. In the time from $1/XI$ to $8/XII$ the number slowly diminished. A few very large females without eggs of any kind were present (Fig. 11). Young brood decreased and by $8/XII$ no brood was observed; there was an ever decreasing number of females with ephippia; most probably old females (Fig. 12) which had formerly produced such, and many females which had thrown them off, and had no new brood in the brood room. Besides there was a number of females propagating parthenogenetically, producing as always about 4—6 eggs; as in all the other samples two sizes of females could commonly be pointed out, one with two eggs, the other with 4—6. The first represent the primiparæ with $T = 1200$.

During the winter 1924—1925 the pond was practically open being only ice-covered a few days in March; the temperature till about $11/IV$ was always $0-3^{\circ} C$.

At this really low temperature the number of *D. longispina* has always been relatively small; the number was large on $28/XII$ and $20/I$, later on the species was extremely rare; in the large samples only 10—20 specimens could be found. It was still the same on $5/V$. During this long period $15/XII-5/V$ females with ephippia had totally disappeared; but strangely enough, a few males were observed. Young brood hardly exists; most probably the number during all the winter months was almost the same; the species was represented by young females (Fig. 13—19) which perhaps had not been impregnated in October—November and which now propagated parthenogenetically. The number of eggs was now commonly only 2—4. A few of the largest of the females had 6 eggs. It is characteristic that the brood room only rarely contained highly developed young ones; almost always eggs which were in the first stages of cleavage or in the first embryonal stage. By $28/IV$ very large females occurred; number of eggs 30—35; simultaneously a few newly hatched young ones were found. By $15/V$ the number was enormously augmented; there were many large females (fig. 22) producing 30—35 eggs. The size of the primiparæ was 11—1200 and they began egg production with 6—8 eggs. Simultaneously many males appeared and in the size 1200 many females now carried ephippia. By $26/V$ the zooplankton consisted almost entirely of *D. longispina* now having an enormous maximum; very many males and females with ephippia (Fig. 27) appeared; these almost all belonged to the size about 1200. By $11/VI$ the sexual period had finished; the species had almost disappeared, a few females with 4—6 eggs besides young ones were still present. The conditions were unaltered up to $20/VIII$. In the last part of September a new sexual period began and this lasted the whole of October.

It is now possible to state the very interesting fact that the very same species in the same locality differs very much in sexuality in two consecutive years. In 1924 it was pronouncedly monocyclic with the sexual period in autumn, in 1925 it was pronouncedly dicyclic with one sexual period in spring and one in autumn. In the first case (in 1924) the number of individuals slowly increased; in the last

case we have two large maxima, one in June and one in Sept.—October interrupted by a very conspicuous minimum.

It is highly improbable that this difference in the form of propagation should be due to inner conditions, much more that it is produced by outer factors. In the first place it seems natural to pay attention to the fact that in the winter 1923—1924 the pond was frozen over in 140, and during the winter 1924—1925 hardly at all. While in 1923 ¹⁰/_{IV} it only had 3° C., it had 10° in 1924 ¹⁹/_{IV}. Furthermore that the summer 1924 was much colder than that of 1925, which was extremely warm, causing a much lower waterline than in 1924. In May 1924 the temperature of the water was hardly ever above 10° C., and in June it only rarely reached 18. In May 1925 it was 10—12 in the first part of the month, and in the last part often near 20° C.; in June it was almost always 20, and in the period near ¹¹/_{VI} often round 23° C. The enormous maximum in spring 1925 coincided with the sudden high temperatures in the last part of May and during most of June. It seems highly probable that the great differences in temperature during the years 1924 and 1925 have in some way influenced the cyclus of *D. longispina* in the said pond, but a more thorough understanding cannot be arrived at.

On the other hand, with regard to the cyclus we can pay attention to the following fact. Whereas *D. l.* during the whole summer 1924 is relatively rare and only has its max. in autumn, in 1925 it has an enormous max. in June. As in 1925 in April and in the first part of May it is even extremely rare, it seems highly improbable that the sudden large max. in spring 1925 should be developed from the small number of wintering females. The most probable supposition is that most of the ephippial material of 1924 has been destroyed during the exceedingly severe winter, and that during the summer months owing to parthenogenetic propagation of the relatively few individuals the species has only slowly developed the autumnal max. with its sexual period. On the other hand in 1925 enormous quantities of ephippia may suddenly have been developed and created the large maximum developed during the time ¹⁵/_V—¹/_{VI}. As the species was exceedingly rare by ⁵/_V, only represented by very large wintering females ($T = 17-1800$), and the water already teemed with ephippia carrying females ($T = 11-1200$) ²⁶/_V, it seems almost certain that the species has passed over into sexual propagation in one of the first generations, perhaps already in the first, after a series of parthenogenetic broods. —

It is further noteworthy that an enormous maximum in spring, followed by a sexual period, is followed by a sudden and almost total extinction in summer, whereas a slight number of animals in spring only propagating parthenogenetically creates a slowly augmenting number of individuals during summer from which the large maximum in spring develops, in other words that ephippial females in June die out after having produced ephippia and do not continue with parthenogenetic propagation. On the other hand the results of the explorations in the autumn of 1924, as well as in the autumn of 1925, seem to show that the ephippial females from the autumnal sexual period do not die out, but, having produced ephippia,

again produce new parthenogenetic broods. Especially the characteristic marks upon the valves of the females producing parthenogenetic broods in Nov.—Decbr. show this conspicuously; but also the slowly increasing size of the ephippial females in Sept.—Nov. points in the same direction. It seems therefore that high temperatures or more probably factors combined with them (mainly variations in chemical composition of the water) upon the same individual may act so as to diminish the parthenogenetic propagation after a sexual period, but at low temperatures so as to accelerate it. —

With regard to seasonal variation this may be said to be almost totally wanting. The whole year round propagation begins when the animal has reached the size 1100—1200 (without spina). The normal size for the female with six eggs is about 13—1400, and this size is unaltered the whole year; the ephippia-carrying females are perhaps a little smaller, but the difference is but slight. The anterior contour of the head is always round; tendency to a galea never appears. $\frac{A + B}{V}$

is the same the whole year, about $\frac{1}{3}$ — $\frac{1}{2}$, and the real length of A differs very little in the young and the old females, only from 30—90, and not regularly during the year. The eye is larger during winter than in summer in the old females, and presents the only conspicuous difference which I am able to find between summer and winter individuals. In the summer individuals the number of lenses is much higher than in the winter animals; they are especially much more free of the pigment, lying as a bright corona round the pigment; in the winter animals they are sunk in the pigment and almost invisible; if their number is really smaller is a question. The spina in the young brood seems to be of the same length during summer and winter, but this is difficult to say, because it is difficult for 100 young ones in summer to get a single one in winter. That the spina is not augmented in size in the ripe animal, and that it is shortest in females which have thrown off an ephippium, is certain; if it be longer in summer than in winter cannot be seen without very extensive variation statistics, but it is certain that the difference can only be very small. —

A more thorough exploration of *D. longispina* in other ponds and smaller lakes would certainly, both with regard to cyclomorphose and propagation, give interesting results differing from the above-mentioned. As mentioned above, as far as my experience goes, the *longispina* races are rare in Cyanophycé lakes and ponds; the localities are so far from each other that it is very difficult simultaneously to carry on regular observations. —

In four of our larger lakes *D. longispina* was found in 1909, and there in races which differed from each other, and very much from those characterising ponds and smaller lakes. — They were studied in my Plancton Investigations 1904—1908. Referring the reader to this work with regard to illustrations and a more thorough account of the results, I shall here only review the main points which cannot be discussed in this connection.

D. longispina forma *lacustris* Viborg lake.

Tab. II.

In Viborg lake which is ca. 330 ha. and about 15—16 m. deep and which is a pronounced Cyanophycé lake with enormous Cyanophycé maxima during the greater part of the year we find a peculiar race of *D. longispina* forma *lacustris*.

The species occurs in spring; it is rather rare till the middle of July, when the maximum occurs; this lasts throughout autumn and the beginning of winter. It is numerous even in January. —

The individuals have no eggs in March, in April about four eggs, in May, 6. Curiously enough in contrast to almost all other plancton-cladocera the number of eggs is always augmented during summer; in July, 5—8; in August—November, 10—12. In November—December the large individuals with 10—12 eggs disappear, but small females producing 1—2 eggs are still numerous. They are empty in Jan.—March and begin egg production after hibernation in April. The race was acyclic in the two years of observation; not a single female with ephippium has been observed, but in June—July a few males have been found.

The cycle has a very peculiar course in this lake. The generation which is born in autumn gets a few broods in December, suspends the egg production below the ice, begins it again in April and is dying out in June. It has almost no cyclomorphose at all.

T, when egg production begins in Nov. is about 1300, $A + B = \frac{1}{2} V$. A 250. When it dies T is 1600—1800. A increases very little; B a little more and the result is very low-crested individuals with $A + B = \frac{1}{3}$ to $\frac{1}{4} V$. All individuals are typical roundheads; in fact they much resemble those from the Hestesko pond. It must be kept in mind that in these winter individuals, which as well in Hestesko pond as in Viborg lake reach about $A = 800 \mu$, A is in Hestesko pond only 100—130, in Viborg lake 250. The more planctonic life in Viborg lake has set its stamp upon the species.

From this winter generation the first summer generation appears in June and a series of summer generations now follow each other. What especially characterises these summer generations is that the size always increases up to November;

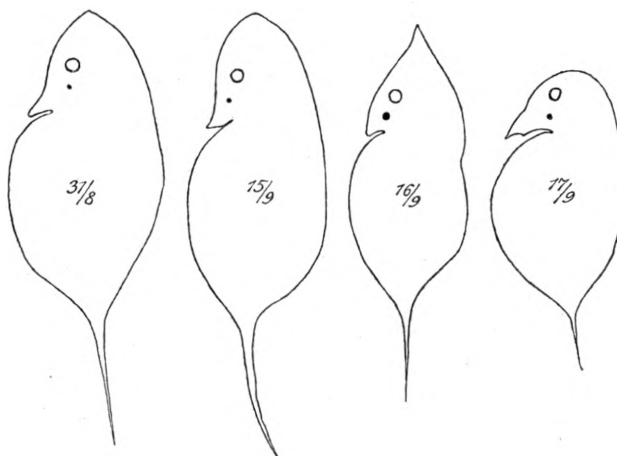


Fig. 2.

Daphnia longispina forma *galeata*, Esromlake; *D. longispina* forma *lacustris*, Viborglake; *D. longispina* forma *lacustris*, Haldlake; *D. longispina* subsp. *D. hyalina* forma *pellucida*, Sorølake. See also Tab. II. 40×

a summer minimum does not exist; the number is always increasing and so also the size, as well from brood to brood, as also from generation to generation. No decline owing to weakening produced by parthenogenetic propagation has been traced. The result is large females with $T = 2400$; the increase is almost exclusively in V which is 1600 and in B 400. A increases to 400 and $A + B$ is therefore $\frac{1}{2} V$. Like the winter generation the summer generations are typical roundheads, but whereas $A + B$ was $\frac{1}{3}$ to $\frac{1}{4} V$ during winter, it is $\frac{1}{2} V$ in summer. The life conditions differing from those in the winter half of the year have induced another and higher form of the head. Another peculiar fact with regard to the Viborg *longispina* is that the growth stages during summer, before they reach maturity, and especially those which belong to the last part of July and to the first part of September, are so high crested that $A + B$ is almost $= V$. $A + B = 400$. $V = 450$. It is only in these high crested summer forms that a distinctly defined point may exceptionally be found, so that the race approaches the *galeata* race. In this form maturity is reached, but during the following months the head is more and more rounded, and when $T = 1800$ every trace of a point has disappeared. In the newly hatched young A is about 150μ during summer, during winter only about 50μ .

D. longispina forma *lacustris* in Hald lake.

Tab. II.

Quite the same form also occurs in Hald lake. The lake is 334 ha; it is much deeper, about 36 m, and has only a short time smaller Cyanophycé maxima, the diatoms and *Ceratium hirundinella* producing the greatest plancton quantities in the lake. —

Even if we find the same form in these two lakes, which so to speak present the greatest extremes which we are able to find in our country, the one with dirty water overfilled with organic matter and with temperatures often reaching $22-23^{\circ}$, the other with extremely clear water and only rarely reaching more than $18^{\circ} C.$, the different life conditions have set their different stamps upon the two races.

In Hald lake the species has no pronounced maxima and minima; it is only for a short time that it belongs to those which predominate in the plancton. It is peculiarly numerous in early spring after the ice has melted; it has its max. in July, then it decreases in number, but this is again augmented in December—January. —

The females carry 3—4 eggs in March; temperature only about $2^{\circ} C.$ In May the number increases to seven, but then it decreases again, being commonly only about 4, often only 1—2. In October all large females are barren, and the winter forms have not begun egg production. This does not take place before November—December; the number of eggs is then 1—2. Ehippia have never been observed; the race may in the two years of observation be regarded as pronouncedly acyclic; only on $\frac{30}{V} 02$ a few males were found.

The cycle differs appreciably from that of Viborg lake. The winter generation is born in Oct.—Nov.; upon maturity in Nov.—Decbr. the size is 9—1500, $V = 800$;

now the peculiar fact is that these small females at temperatures near zero produce very many small broods with only 1—2 eggs in the egg sets. Owing to this fact the species is remarkably numerous in winter. In March the number of eggs has increased to 4, in June to 6—7. Then the generation dies out. From Nov. to June the size has only been altered very little; in October 9—1500, in June 1600. This generation has almost no cyclomorphose at all. In Oct.—Nov. $A + B$ is ca. $\frac{1}{2} V$, in Jan. it decreases to $< \frac{1}{2} V$, in May to $\frac{1}{3} V$ as the growth of A does not keep pace with that of V . During the whole period A is at most 240, but may in spring go down to 120. All individuals are typical roundheads.

The summer generations set in in June; there is a maximum in July but then the number decreases. In the summer generations, the size of which never exceeds 1800, A increases slowly from June to September; from 160 to 320 and then in September to 480; then $A + B > \frac{2}{3} V$. In July—September individuals with pointed heads may occur among the egg-producing sizes, but even then the head has mostly a rounded character; typical *galeata* forms do not occur. The summer forms are all in all more slender, the winter forms more clumsy; but there is not as in Viborg lake a regular increase in size in the summer months. In October there is a very conspicuous gap between the barren forms now dying out of 1800 and the young ones of about 1200, which will begin egg production a fortnight later.

The growth stages are always roundheads during winter, A being about 160. From $\frac{11}{VI}$ to $\frac{25}{VI}$ individuals with pointed heads appear. In a size of 1100 $A + B$ is $> \frac{1}{2} V$ and A may in August reach 480, $A + B$ being then nearly $\frac{2}{3} V$. During this time only primiparæ with pointed heads occur. The course of development changes in August; then high individuals with pointed heads only occur amongst the oldest sizes and A does not exceed 320. The head of the newly born young ones during the period $\frac{11}{VI}$ to $\frac{25}{VI}$ suddenly passes from round to pointed; in summer all the young have pointed heads, in winter all round. The pointed head is still to be found in the young females which produce the first egg set, during the following months the head is more rounded, but it must be emphasised that A is not therefore shorter, on the contrary, it may often grow higher.

However much these two races resemble *D. longispina* from Hesteko pond, especially during winter, the planctonic life has influenced them both. It seems as if they are practically pronouncedly acyclic; during the summer half of the year the young ones are born with an A about $\frac{1}{3}$ higher than during winter; this difference we do not find in the young ones from summer and winter in Hesteko pond. Neither is there any appreciable increase of A during growth in the summer half of the year before or after maturity, whereas this is very pronounced in the races from the two lakes. —

Of the two races that of the lake which has most the character of a pond (Viborg lake) is most nearly related to that of Hesteko pond. We do not find any summer minimum here; the size is exceedingly large; it does not diminish, on the contrary it increases during the whole of the summer; the number of eggs is re-

markably high and the number in which the species hibernates is not great; all this still belongs to the characters marking life in ponds. On the other hand we have in Hald lake a *longispina* race with a summer minimum; the size is not particularly large; the maximum, 1800 μ , is reached in July, and is not augmented later on; more thorough explorations will most probably show that it diminishes; the number of eggs is but small, during most of the year not exceeding about 4. The species hibernates below the ice as numerous small females with egg sets of 1—2.

D. longispina forma *galeata*. Esrom lake.

Tab. II.

D. longispina forma *galeata* is one of the main planctons in Esrom lake. This is one of our largest lakes, being 1750 ha.; the maximal depth is about 25 m. The form was previously termed *D. galeata* G. O. S. by P. E. MÜLLER (1868 p. 118) and was later by LILLJEBORG referred to var. *galeata*; yet in his opinion it differed so much from the latter that it must be referred to a special variety: *ambigua* (1900 p. 121) "welche sich am meisten von allen der Untergattung *Hyalodaphnia* nähert".

In Esrom lake var. *galeata* has two well marked maxima in spring and autumn, and two well marked minima in summer and winter. The specimens which are found in March—April after the melting of the ice, are empty; in May and the first part of June the females carry a large number of eggs (30—35); in early summer the number is only 4—6; this diminishes in July to 3—4; in August to 3 and in September to 2—1; this number persists until December, when most individuals are empty. In January only a few individuals have been seen with one egg.

It really seems as if the species in Esrom lake should be designated as dicyclic. Ehippia were found in October 1900 and in July 1902. Their number was always small and during the whole of 1901 not a single ehippial female was found. There is the possibility that the samples have always fallen between two sexual periods, but that this should be the case all three years is highly improbable; moreover, I have never in the samples found females which have carried ehippia, and in the following years 1903—1925 in which I have very often taken samples in Esrom lake, I have only very rarely seen females with ehippia. It seems as if the species mainly propagates parthenogenetically, but has reminiscences of a sexual period in July and in October. It is, however, possible that an exploration based upon samples taken every tenth day, and carried on with horizontal closing nets fishing at a depth of about 20 m, would show that the sexual propagation has greater significance than I have supposed.

The cycle runs as follows. The winter generation begins with a maximum of young females with T about 1500. They carry 1—2 eggs. A is about 250 and A + B only $\frac{1}{3}$ V. In the winter months, at all events in those winters when the lake has been icebound for 2—3 months, the number of wintering individuals is remarkably small; there is a pronounced minimum in early spring. The wintering females con-

stantly increase but the increase belongs almost only to V. The ratio $\frac{A+B}{V}$ therefore steadily decreases. During winter the females reach a size of 1900—2000; they are almost always roundheaded. They carry only one or two eggs; in March—April they are barren. In the course of April they increase to the size of ca. 2400 and now produce very high egg sets (30—35). These very large females with A + B almost only $\frac{1}{4} V$ disappear in June. In the last part of May there are two conspicuous forms, the large females of the size 2400, and many young females only about 1500. In these forms A is about 320 and $A + B < \frac{1}{2} V$. During the period June—Sept. T constantly increases and reaches about 2000, but now the increase applies almost only to A which reaches about 640. Thus the ratio $\frac{A+B}{V}$ constantly increases and in the young females almost reaches 1. The typical forma *galeata* with distinct high points occurs only from the end of June. These individuals produce a summer maximum perhaps limited by a sexual period. Then a pronounced summer minimum sets in; during this the forma *galeata* is the main form, later on in the last part of August the typical *ambigua* Lillj. prevails, but many transitional stages occur. All these summer forms are characterised in comparison with the winter forms by their slender form, their long spina, small height and a slight curvature of the ventral and dorsal contours. Slowly in Oct.—Nov. the autumn maximum, mainly deriving from smaller females with T = 1600 begins. These smaller females, always producing very few eggs, reach maturity before winter at T = 1500, and reach a size of about 1900. It is the last broods of this generation which in an always decreasing number hibernate and begin propagation with very high egg sets in May.

The typical *ambigua* and *galeata* forms become rarer and rarer, uniformity in appearance begins to assert itself; already in September pronounced roundheads appear, these prevail during winter; in spring (May) all individuals are roundheads.

— With regard to the growth stages during Oct.—June, $\frac{A+B}{V}$ remains almost unaltered during growth or V increases more than A + B (A = 2—300). Only during the time ca. $\frac{15}{VII}$ to $\frac{1}{IX}$ A + B increases more than V, and often become = V. A may reach even 600. In young newly hatched brood there is hardly any seasonal variation; it is always roundheaded and A is 130—160. —

Thus the seasonal variation in Esrom lake occurs principally as the result of the uneven and irregular increase in A during growth at the different seasons. At hatching this is about 130 the whole year round; during growth it does not exceed 300 in winter, in summer it rises to about 600. In the series of winter generations both rounded and pointed crests occur; but only in the series of summer generations are the sharply marked high points developed during growth. In the egg producing stages a seasonal variation occurs, especially in the summer forms where the point of the *galeata* forms decreases during the months in autumn.

Also with regard to this form we see that during winter the difference between the individuals in Hesteko pond and Esrom lake is really but small. The main difference is also here that whereas A at birth in Hesteko pond is only 100—130 at birth, it is 130—160 in Esrom lake and may during growth reach 200—300. The great differences only appear in the summer months. — It is during this time that the form *ambigua* appears, which also in the opinion of LILLJEBORG of all *D. longispina* races is nearest to *cucullata*. It is highly remarkable, that *D. longispina* as well in this as in other forms is able the whole year round to live in the same medium as *cucullata*; as most probably they are members of the same "swarms" formed by them both, and nevertheless at highest summer temperatures *D. l.* does not seem to show any cyclomorphose at all. —

If we will now try to cast a glance at the different races of *D. longispina* as we have now become acquainted with them in the ponds with peaty water, in the Cyanophycé ponds (Hesteko pond) in a Cyanophycé lake, Viborg lake, and in three of our lakes with no pronounced Cyanophycé maxima and with clear water, there cannot be any doubt that just in this species we are able to see how, originally having its home in very small ponds, it has accustomed itself to life under quite different conditions even in the pelagic region of some of our largest lakes (e. g. Bodensee). By this accommodation it has been altered biologically and morphologically; these alterations we are able to follow step by step. Derived from *D. pulex* which, leaving the littoral region, accommodated itself to the central parts of our ponds, an accommodation which caused the disappearance of the pecten on the claws and which in many localities is going on even now and may be clearly shown; as *D. longispina*, it got a new home in the central part of small waters. Perhaps owing to the great difference in the chemistry of these ponds especially with regard to their amount of humic acid or organic matter, forms appeared which differ a little from each other. All in all the character of these pond races is the same, and the pelagic life has only to a very slight degree altered them. There is no conspicuous cyclomorphose. These *longispina* forms are somewhat slender, the spina is longer, they are rather hyaline, especially during summer; during autumn often red. There is a pronounced sexual period during autumn, now and then another in spring; the ratio $\frac{A + B}{V}$ is almost the same the whole year round. There is always a pronounced minimum in winter and spring; in cold winters the animals may in spring only begin propagation from specimens hatched from ehippia. The number of eggs during summer only rarely decreases to 1—2.

From these pond races originate the lake races. These races differ more or less from the pond races; the new life conditions have given them their special stamp biologically as well as morphologically, more or less pronounced in the different races, but common to them all by the same marks in which they all differ from the pond races.

The most peculiar mark is perhaps the tendency to acyclic in my opinion

caused by selection; the ephippial carrying females are too heavy and are in this way forced downwards in layers of water where the life conditions are bad. This is corroborated also by other authors e. g. WAHLBERG (1913 p. 77). Whether or not the explanation is correct, the observation itself may be regarded as an indisputable fact. Upon this phenomenon again depends the possibility of fixation of racial characters, which produced the peculiar fact, that each lake so to speak got its own race, formerly regarded as distinct species: *lacustris*, *galeata*, *pellucida*, *ambigua* etc. — Common to all these races is the hyalinity, the small eye, a spina which in most cases is longer than in the pond races, and the small number of eggs; this is especially due to the summer forms, where the number of eggs often goes down to only one; further, the fact that the races owing to the loss of sexual periods, and formation of ephippia in smaller or larger quantities, hibernate below the ice; the number of hibernating individuals differs from lake to lake; most probably also from year to year. It is greatest in winters with high temperatures. Common to all the races is also that the young the whole year round are born with A higher than in the pond races. During winter the ratio $\frac{A+B}{V}$ is only altered in the way that it is only V which is increased, $A+B$ not at all or very little; as young ones and old ones the specimens are mainly typical roundheads. During winter the ratio therefore gets smaller and smaller. As the racial stamp especially manifests itself in the greater or less development of A , and in the contour of the head, and this being almost always more or less flattened or round during winter, the different races at this season have no racial stamp at all and differ only from many of the typical pond races mainly by a somewhat greater hyalinity.

In summer most of the lake races differ very much from the pond races. When the temperature has reached 14—16° C., in the course of 2—3 weeks A is augmented very considerably; this is due firstly to the fact that the young ones are born with a higher A than during winter, secondly that during the growth-stages $A+B$ is augmented more than V . The result is therefore that the ratio $\frac{A+B}{V}$ always increases during the summer and may reach 1., and secondly because $A+B$ even after the stage of maturity has been reached after the moults steadily increases to a certain point. In all these respects most of the lake races coincide; it is on the formation of the crest, on the contour of the heads, just that point upon which formerly the many species were created, that the racial stamp depends, causing the peculiar phenomenon that every lake has its own race. Whether these racial characters are hereditarily fixed, or may be merged in each other when the races are brought under other life conditions, we do not know. —

In lakes which are never icecovered, e. g. the lake of Lugano, STEINER (1912 p. 92) has shown that the species, as often also in our latitudes, is perennial, but also that the species during winter does not fall back to the typical roundheaded form common to all our lakes. "Eine solche Einheitlichkeit in der Kopfform (as

in the Baltic lakes) der Wintertiere herrscht im Luganer See nicht; trotz Temperaturen von 4.8° bis 5.6° sind stets mehrere wohlumschriebene Formen vorhanden, die sich auch im Sommer ganz verschieden verhalten und in ihrer Differenziation lange nicht ausschliesslich hohe Helme aufweisen". This observation has its great theoretical significance.

Daphnia longispina subsp. *hyalina*.

Tab. II.

The subspecies *D. hyalina* which seems to play a prominent part in several large southern lakes (e. g. Bodensee), but which seems to be exceedingly rare in our country, has only been found in two Danish lakes: Sorø lake and Tjustrup lake and here in the peculiar form *pellucida*. This form is mainly characterised by its sharply projecting rostrum, shaped like a parrot's beak, and its evenly rounded head. In both lakes it is rare, most probably to be found the whole year round, having a sexual period in October—November. It is a pronounced plancton organism; for such a cyclomorphose should have been expected; the samples, however, show clearly that the animals do not show any trace of that. During the whole year T is 15—1700. A + B is $\frac{1}{2}$ — $\frac{1}{3}$ V. On hatching A is ca. 100; in the egg producing stages 160—240. —

It is of great theoretical interest to find, in lakes which contain enormous quantities of *D. cucullata*, showing a normal cyclomorphose, a very closely related species which can live in the pelagic region of the same lake and without showing any cyclomorphose.

D. cucullata G. O. Sars.

The next step in the development from littoral forms to full planctonic life is found in the species *D. cucullata*, formerly determined *Hyalodaphnia cucullata*. It is especially in winter difficult to distinguish it from *D. longispina*. As, however, the pigment spot is commonly invisible in *D. cucullata* and visible in *D. longispina*, and especially as the antennæ are always placed upon the tip of the rounded rostrum in *D. cucullata*, whereas in *D. longispina* they are almost always placed on the ventral side of the head away from an almost always acute rostrum, it is permissible to keep the two species distinct. This is so much the more correct as the two species biologically differ very much from each other. —

Whereas *D. longispina* mainly occurs in small waters, *D. cucullata* is the pronounced lake form which only very rarely occurs in smaller ponds. Whereas *D. longispina*, as far as my experience goes, commonly reaches its greatest size in ponds, *D. cucullata* produces dwarf races there; the largest races inhabit the pelagic region of larger lakes. Whereas *D. longispina* as a plancton organism in larger lakes so to speak in every lake produces its special race with a rather characteristic racial stamp, the *D. cucullata* races from larger lakes commonly resemble each other much more; they differ a little with regard to size, and especially with regard to

the bending of the crista (*procurva*, *retrocurva*); greater differences do not commonly occur.

All in all *D. cucullata* is morphologically much more adapted for pelagic life than *D. longispina*. It is commonly smaller than this; it is always extremely hyaline; the system of crossing ridges of the valves is very little pronounced; the eye is extremely small, the lenses are larger and rise freely above the pigment; the whole form is very slender, especially during the summer half of the year; only the wintered females in May have a more clumsy form. In the summer half of the year the number of eggs hardly ever rises above 2—3, only the wintered females have a higher number in May. The races are never or very rarely dicyclic; in our country dicyclic races have never been found; monocyclic races occur but acyclic races are very common. Common to the species in all hitherto explored lakes is a pronounced cyclomorphose. Whereas $A + B$ during winter and early spring is often only $\frac{1}{4} V$, during summer it is often $> V$, the length of A during winter being only about 80μ ; in summer it may reach 700 in the same lake.

The cyclomorphose has been thoroughly studied in many lakes; e. g. in nine of our Danish lakes. It is now well known and drawings of it are often found in text books of different kinds. After 1908, when the Plancton investigations appeared, in which I tried to gather all that we at that time knew about *D. cucullata*, its morphology and biology, very many explorations have been carried on. Of all our freshwater plancton organisms it is perhaps the most used and best studied. In an excellent paper WAGLER (1923 p. 41) has gathered all that we know with regard to the systematics and geographical distributions; furthermore he has brought our knowledge of its dependence on the environments, its physics and chemistry a great step forward. We shall often return to this paper in the following.

The lake of Frederiksborg castle is one of the smallest of our lakes in which *D. cucullata* has hitherto been observed. The lake is really only a pond. Its size is only 200 ha.; its depth only 3—4 m. From June to October the water contains enormous quantities of *Cyanophyceae* (*Clathrocystis*) which lie as a scum upon its surface. Before the *Cyanophycé* maximum sets in, the plancton is an almost pronounced Zooplankton, consisting of *Diaptomus graciloides*, *Cyclops strenuus*, *Bosmina longirostris* and *Rotifera*; *Cyanophyceae* are always present and during spring and early summer *Asterionella gracillima*, and in some years, *Volvox globator* may play a certain role. From the last part of June, of the *Rotifera* only *Pompholyx* gets any significance; together with *D. cucullata* occur *Leptodora* and *Daphnella*; the *Ceriodaphnia* and *Ceratium hirundinella* are absent. The *D. cucullata* race from the lake of Frederiksborg castle has played a rather important role in the limnological literature owing to the studies of WOLTERECK and his pupils. An account of its cyclomorphose in this lake has not, however, been hitherto given, especially because I saw that it was very nearly related to those which I have studied in larger lakes. —

Only a few hundred m. from this lake in the Royal garden lies the above-named little pond, the so-called Hestesko pond. Many years ago, already in 1900,

a *D. cucullata* race was found here, differing very much in form and life from the race of Frederiksborg lake. The pond was now visited every year and often in the summer months. The species was always rare, and I often got samples in which it was not detected. It was obvious that I had here to do with a peculiar dwarf race; a closer study was not taken up before the years 1923—1925. The following is the result of this study. As I supposed that it was of interest to get an account of the cyclomorphose the whole year round in the lake of Frederiksborg castle, partly because this race has been studied so much in the laboratories, partly because this little lake has an intermediate stage between the Hestesko pond and one of the nine lakes formerly explored, I have for the same years undertaken a regular study of *D. cucullata* in this lake. I was so much the more induced to do so because the two waters lie so very near each other and each is provided with its own race differing very much from the other.

The Hestesko pond is a very small pond; the circuit is only about 300 m., its depth, only $\frac{1}{2}$ —1 m.; the plancton quantities are all the year round quite enormous, in summer mainly Cyanophyceae; an account of the plancton will be published later on.

We will first consider *D. cucullata* in the lake of Frederiksborg castle and later in the Hestesko pond. —

D. cucullata. The lake of Frederiksborg castle.

Tab. I.

Dato	T	A	B	A + B	V	$\frac{A+B}{V}$	S	H	eggs	Fig.
1924 $\frac{5}{5}$	823	84	118	202	621	$\frac{202}{621}$	336	420	0	1
$\frac{16}{5}$	1092	84	168	252	840	$\frac{252}{840}$	336	672	10	2
$\frac{23}{5}$	974	134	168	302	672	$\frac{302}{672}$	336	504	0	3
$\frac{29}{5}$	1172	134	168	302	840	$\frac{302}{840}$	504	672	8	4a
$\frac{29}{5}$	1126	252	168	402	706	$\frac{402}{706}$	452	588	4	4b
$\frac{29}{5}$	974	252	134	386	588	$\frac{386}{588}$	420	338	0	4c
$\frac{11}{6}$	1404	168	252	420	984	$\frac{420}{984}$	420	672	12	5a
$\frac{11}{6}$	1126	252	168	420	706	$\frac{420}{706}$	454	504	7	5b
$\frac{11}{6}$	1008	336	168	504	504	$\frac{504}{504}$	420	336	1	5c
$\frac{17}{6}$	1404	252	168	420	984	$\frac{420}{984}$	420	588	9	6a
$\frac{17}{6}$	1092	336	168	504	588	$\frac{504}{588}$	420	420	2	6b
$\frac{25}{6}$	1260	336	168	504	756	$\frac{504}{756}$	420	504	9	7a
$\frac{25}{6}$	1142	470	168	638	504	$\frac{638}{504}$	420	420	2	7b
$\frac{2}{7}$	1596	588	168	756	840	$\frac{756}{840}$	420	588	7	8a
$\frac{2}{7}$	1092	420	168	588	504	$\frac{588}{504}$	420	420	2	8b
$\frac{9}{7}$	1260	504	168	672	588	$\frac{672}{588}$	420	504	4	9a
$\frac{9}{7}$	974	420	134	554	420	$\frac{554}{420}$	336	336	0	9b
$\frac{18}{7}$	1344	588	168	756	588	$\frac{756}{588}$	336	370	2	10a
$\frac{18}{7}$	974	420	134	554	420	$\frac{554}{420}$	336	269	1	10b
$\frac{25}{7}$	1142	420	134	554	588	$\frac{554}{470}$	420	420	5—6	11a
$\frac{25}{7}$	1142	420	134	554	470	$\frac{554}{470}$	420	336	2	11b
$\frac{25}{7}$	504	168	84	252	252	$\frac{252}{252}$	252	168	0	
$\frac{28}{7}$	622	252	84	336	286	$\frac{336}{286}$	286	168	0	

Date	T	A	B	A + B	V	$\frac{A+B}{V}$	S	H	eggs	Fig.
18/8	1260	504	168	672	588	$\frac{672}{588}$	420	420	1-3	12a
18/8	974	420	134	554	420	$\frac{554}{420}$	470	252	1	12b
20/8	1260	504	168	672	588	$\frac{672}{588}$	420	336	1-4	13a
20/8	1008	420	168	588	420	$\frac{588}{420}$	336	252	1	13b
20/8	861	370	134	504	357	$\frac{504}{357}$	336	336	1	13c
1/9	1495	420	235	655	840	$\frac{655}{840}$	420	588	5-6	14a
1/9	1478	588	218	806	672	$\frac{806}{672}$	504	420	4	14b
1/9	1108	470	134	604	504	$\frac{604}{504}$	420	336	0	14c
1/9	861	370	134	504	504	$\frac{504}{504}$	336	420	E.	14d
10/9	1344	370	134	672	672	$\frac{672}{672}$	168	504		15a
10/9	1008	504	168	504	504	$\frac{504}{504}$	336	420	E.	15b
10/9	1092	336	168	588	336	$\frac{588}{336}$	336	420	2-3	15c
10/9	1092	420	168	588	504	$\frac{588}{504}$	336	252	0	15d
25/9	1260	420	168	588	672	$\frac{588}{672}$	336	504	4	16a
25/9	940	302	134	436	504	$\frac{436}{504}$	420	370	1	16b
25/9	656	202	118	320	336	$\frac{320}{336}$	420	252	0	16c
15/10	1176	336	168	504	672	$\frac{504}{672}$	336	504	Ep.	17a
15/10	907	235	168	403	504	$\frac{403}{504}$	202	336	1	17b
15/10	588	168	84	252	336	$\frac{252}{336}$	336	252	1	17c
24/10	1260	336	168	504	756	$\frac{504}{756}$	336	588	E.	18a
24/10	924	168	168	336	588	$\frac{336}{588}$	336	370	2	18b
24/10	756	168	168	336	420	$\frac{336}{420}$	336	336	1	18c
24/10	454	118	84	202	252	$\frac{202}{252}$	252	168	0	18d
1/11	1008	168	168	336	672	$\frac{336}{672}$	336	336	4	19a
1/11	770	101	134	235	588	$\frac{235}{588}$	336	370	1	19b
21/11	1260	252	168	420	840	$\frac{420}{840}$	336	588	0	20a
21/11	770	101	134	235	588	$\frac{235}{588}$	336	376	1	20b
21/11	656	118	118	236	420	$\frac{236}{420}$	252	330	0	20c
31/12	1008	84	168	252	756	$\frac{252}{756}$	202	588	2	21a
31/12	890	84	134	218	672	$\frac{218}{672}$	252	504	0-2	21b
1925 14/1	1008	168	168	336	672	$\frac{336}{672}$	538	588	2	22a
14/1	857	118	151	269	588	$\frac{269}{588}$	336	504	0-1	22b
14/1	806	84	134	218	588	$\frac{218}{588}$	336	504	1	22c
30/1	1024	134	168	302	742	$\frac{302}{742}$	252	588	0	23a
30/1	806	84	134	218	588	$\frac{218}{588}$	336	504	0	23b
5/2	924	84	168	252	672	$\frac{252}{672}$	252	588	3	24a
5/2	873	67	168	235	638	$\frac{235}{638}$	268	420	0	24b
18/2	924	84	168	252	672	$\frac{252}{672}$	330	470	0	25a
18/2	806	84	134	218	588	$\frac{218}{588}$	336	504	1	25b
2/3	840	84	168	252	588	$\frac{252}{588}$	336	588	0	26
2/4	1008	84	168	252	756	$\frac{252}{756}$	252	924	2	27
7/4	1008	84	168	252	756	$\frac{252}{756}$	252	588	2	28
28/4	924	84	168	252	672	$\frac{252}{672}$	252	504	1	29
5/5	1142	134	168	302	840	$\frac{302}{840}$	504	672	5	30
12/5	974	252	134	386	588	$\frac{386}{588}$	420	336	0	31a
12/5	940	134	134	268	672	$\frac{268}{672}$	504	588	5	31b
12/5	656	202	118	320	336	$\frac{320}{336}$	420	252	0	31c
24/5	1496	218	168	486	1008	$\frac{486}{1008}$	504	840	13	32a

Date	T	A	B	A + B	V	$\frac{A+B}{V}$	S	H	eggs	Fig.
24/5	1176	252	168	420	756	$\frac{420}{756}$	504	672	15—8	32b
24/5	1008	286	134	420	588	$\frac{420}{588}$	420	420	2	32c
24/5	974	252	134	386	588	$\frac{386}{588}$	420	336	2	32d
24/5	974	336	134	470	504	$\frac{470}{504}$	336	420	0	32e
16/6	1344	504	168	672	672	$\frac{672}{672}$	504	168	4	33a
16/6	907	420	168	588	504	$\frac{588}{504}$	336	336	1	33b
16/6	1092	235	168	403	504	$\frac{403}{504}$	336	202	1	33c

D. cucullata. Primiparæ.

1924	29/5	974	252	134	386	588	$\frac{386}{588}$	420	336	1	4c
	29/5	856	134	134	268	588	$\frac{268}{588}$	420	336	1	
	11/6	1008	336	168	504	504	$\frac{504}{504}$	420	336	1	5a
	17/6	1092	336	168	504	588	$\frac{504}{588}$	420	420	2	6b
	25/6	1142	470	168	638	504	$\frac{638}{504}$	420	420	2	7b
	2/7	1092	420	168	588	504	$\frac{568}{504}$	420	420	2	8b
	9/7	974	420	134	554	420	$\frac{554}{420}$	336	336	0	9b
	18/7	974	420	134	554	420	$\frac{554}{420}$	336	269	1	10b
	25/7	974	370	134	504	470	$\frac{550}{588}$	336	302	2	11b
	18/8	974	420	134	554	420	$\frac{554}{420}$	470	252	1	12b
	20/8	861	370	134	504	357	$\frac{504}{357}$	336	336	1	13a
	1/9	1108	470	134	604	504	$\frac{604}{504}$	420	336	1	14c
	16/9	1092	420	168	588	504	$\frac{588}{504}$	336	420	1	15c
	15/10	907	235	168	403	504	$\frac{403}{504}$	202	336	1	17b
	24/10	756	168	168	336	420	$\frac{336}{420}$	336	336	1	18c
	14/11	770	101	134	235	588	$\frac{235}{588}$	336	370	1	19b
	21/11	770	101	134	235	588	$\frac{235}{588}$	336	376	1	20b
	21/11	770	101	134	235	588	$\frac{235}{588}$	336	370	1	20c
	31/12	890	84	134	218	672	$\frac{218}{672}$	504	252	2	21b
1925	14/1	806	84	134	218	672	$\frac{218}{672}$	420	252	1	22a
	30/1	806	84	134	218	588	$\frac{218}{588}$	504	336	1	23b
	5/2	873	67	168	235	638	$\frac{235}{638}$	420	286		24b
	18/2	806	84	134	218	588	$\frac{218}{588}$	504	336		25b
	5/5	806	168	134	302	504	$\frac{302}{504}$	420	336		30b
	12/5	904	134	134	268	672	$\frac{268}{672}$	588	504		31b
	24/5	1008	286	134	420	588	$\frac{420}{588}$	420	420		32c
	24/5	975	252	134	386	588	$\frac{386}{588}$	336	420		32d
	16/6	907	235	168	403	504	$\frac{403}{504}$	220	336		

D. cucullata. Neonatæ.

see Fig. 3 p. 138.

1924	5/5	520	134	84	218	302	$\frac{218}{302}$	336	202		
	12/5	520	134	84	218	302	$\frac{218}{302}$	336	202		
	27/5	554	168	84	252	302	$\frac{252}{302}$	336	202		
	10/6	672	252	84	336	336	$\frac{336}{336}$	336	168		
	25/7	638	252	84	336	302	$\frac{336}{302}$	336	168		
	20/8	638	252	84	336	302	$\frac{336}{302}$	336	118		
	9/9	520	134	84	218	302	$\frac{218}{302}$	336	168		
	11/11	454	118	84	202	252	$\frac{202}{252}$	252	202		
	31/12	403	67	84	151	252	$\frac{151}{252}$	252	202		

In 1923—1924 the lake was frozen from $1/XII$ to $17/IV$. During winter samples were taken from shore in an opening in the ice, but no specimens were observed. By $27/IV$ not a single specimen could be found. By $5/V$ the first specimens (only two) appeared, and till $20/VI$ the species was extremely rare. The zooplankton consists of *Cyclops strenuus* and *Rotifera*; in none of the large samples were found more than about 10 specimens. Those which appeared in May were typical roundheads (Fig. 1—2), with $T = 800—1000$; $A + B$ is always $< 1/2 V$ and may be $1/3 V$. A is only 80—130. $V = 6—800$. The form was very clumsy. The number of eggs did not exceed 10. H was 650—700 in the largest individuals.

At the beginning of June these roundheads disappeared and new forms appeared. They were almost of the same length, but V was now not 6—800, but commonly below 600; on the other hand, A was now 150—200 and $A + B > 1/2 V$. These forms were all very slender; H was commonly only 500. All these forms had conspicuously pointed crests and a straight feebly convex ventral contour of the head. They began egg production with T about 1000 and V 600 (Fig. 5c). The number of eggs was but small, 2—4. A few larger forms with $T = 1460$ and $A + B = 420 < 1/2 V$ were found, they had very pointed heads, were rather clumsy; H near 700 (Fig. 6). They produce about 12 eggs. During the whole time the neonatæ had $A + B$ about $2/3 V$ and A about 130 μ . I am inclined in the roundheads from $5/V$ to see the rest of the wintering females; in the forms of fig. 5ab to see their brood; and in the others to see material which is mainly hatched from ephippia and just now have begun egg production. Forms such as Fig. 5a were still found by $25/VI$ (Fig. 7a) with a somewhat higher A . At this time, however, occurred the conspicuous alteration. T only rarely exceeded 12—1300, but $A + B$ was now in all sizes almost always $= V$ and very often $> V$ (Fig. 9a—13a). The increase was not due to V which rarely exceeded 700 and in July—August commonly only reached 600. On the other hand, A reached 500 to 580. Maturity was now reached at $T = 900—1000$, but H was not as in May at the same stage 500, but only 400—420. These specimens were, even if they were larger than in May, in reality much smaller and especially much slenderer. In the broodroom there was not much room and the number of eggs was not more than 1—2. A was $\geq V$ about 400—420. These forms were now the main forms in the plancton in July—August. The number regularly increased; forms of the size 15—1600 (Fig. 8a) with $A + B$ a little smaller than V and a somewhat greater fertility might occur, but the number of these larger forms was not large. During summer the young ones were born with $A + B = V$ and A about 250. At the beginning of September an alteration again began (Fig. 14a). The size was augmented. T was regularly augmented, and even if this was not the case with A , it was in a much higher degree the case with V which was very often about 850—900. Simultaneously A decreased, especially in the older specimens, and was almost always below 400—420. In the older form $A + B$ was therefore often a little below V and never more. It was this size which on $16/IX$ (Fig. 15a) showed the first ephippia; they were older summer forms which,

having produced a series of parthenogenetic broods, now began sexual propagation; for every moult A was reduced. During September the young ones were hatched with $A + B = \text{about } \frac{2}{3} V$ and A 134; during growth $A =$ or a little $> V$ (Fig. 15c). Maturity was reached at $T = 1000$, but already now A was a little below 400; a shortening has taken place during the last moults. The maximum occurred in September; the main forms are shown in 14a, 14b and 16a. During the period $^{20}/\text{IX} - ^{15}/\text{X}$ the sexual period set in. Enormous amounts of ephippia were produced; then from $^{15}/\text{X}$ the number of specimens decreased, but during the whole year *D. cucullata* was present in the lake. By $^{21}/\text{XI}$ ephippia were still found, but later on only very rarely. During the time $^{15}/\text{X}$ to $^1/\text{XI}$ the surface of the lake was covered on calm days with innumerable small dark points. These were the ephippia which were later on, together with staloblasts of bryozoa and resting eggs of *Brachionus pala*, swept into the bays of the lake where they would either be frozen in the ice or thrown up above the waterline by gales; they would again be hatched by the waves in spring. The ephippia-carrying females (Fig. 17a and 18a) had $T = 1150 - 1260$. $A + B$ is now only about $\frac{2}{3} V$ and A only about 330. Simultaneously with them rather many young females in size only about 900, $A + B$ only $\frac{2}{3} V$, and A only 168, appeared (Fig. 17b). In comparison with their small length they were remarkably clumsy, $H = 350 - 400$. In this size they produced the first set of eggs, which never contained more than 1—2 eggs.

The ephippial females died out during autumn and winter; some few were still alive in December but were then commonly empty or produced only few eggs (1—3) in proportion to their large broodroom. A female with ephippium has been observed in the last part of December. As late as $^{24}/\text{X}$ young ones with pointed crests and $A + B$ at all events $= \frac{1}{2} V$ were born; during growth $\frac{2}{3} V$ was reached, from December this was no more the case. During the long period from $^{15}/\text{XII}$ to $^{18}/\text{IV}$ 1925 in which the temperature of the water was always between 0 and +3, the lake being ice-covered only two times in about two days, the species was extremely common. The size was always the same (Fig. 21—27). T is about 900—1000. $A + B$ about 240, $< \frac{1}{3} V$. A was but 80—100, very rarely 160. The crista was extremely low, commonly the animals were typical roundheads. The forms were rather clumsy, the height being about 500. The animals began egg production at $T = 900$ but the number of eggs was only 1 or 2, very rarely 3. The eggs were developed; in very many of the broodrooms there were young ones ready to break out, and in the waterlayers were found young brood but only very rarely. This young brood had only $A = 60$ and $A + B$ a little more than $\frac{1}{2} V$. They were typical roundheads. The propagation went on, but unquestionably very slowly. Nevertheless the number did not seem to decrease any more; at the beginning of March it seemed a little higher. The growth went on extremely slowly. The size of the primiparæ being about 8—900, it was only augmented during winter by about 100μ , and this augmentation fell almost entirely upon V. If these small females did not grow considerably in length, they grew so much the more in height. It

often reached 600 (Fig. 23a). The result is very clumsy forms, much more clumsy than those from July—August, the height being then only about 350—400, and even in the larger females of the size 1300—1400 not reaching more than about 400.

Whereas the lake was frozen during the winter of 1923—1924 for about 140 days and almost totally ice-covered for almost 4 months, during the whole winter 1924—1925 it had no ice at all before $^{13}/_{III}$. During the time $^{13}/_{III}$ to $^{25}/_{III}$, i. e. 12 days, the main part of the lake was ice-covered, but in the middle of the lake there was an opening inhabited by about 70 ducks, the lake was perhaps totally ice-covered only during one single night.

It might now be expected that *D. cucullata* would show very conspicuous differences as well with regard to frequency as to propagation during the two winters of which the lake in one was ice-covered for about 140 days, in the other practically open the whole time. I had especially expected that the species should be much more common in the spring of 1925 than in the spring of 1924. Sad to say all my calculations were wrong, and the opposite was actually the case.

Still at the beginning of March the species was rather common. The size and form was the same as in December, only the forms were more clumsy; all ephippial females and all males disappeared in December. Already at the beginning of January many females had no eggs, having not begun egg production. During the whole of January and February most females had no eggs and never more than one or two. By $^{2}/_{IV}$ large samples were taken from the boat; the temperature of the water was 5° at the bottom, 7° at the surface. In these large samples was found only one single *Daphnia* (Fig. 27) with dimensions quite like the foregoing.

In April three large samples (Fig. 27—30) were taken, but always only one single specimen could be found; the samples were examined for more than an hour. During this long time in which the temperature of the water rose from about $5-7^{\circ}$ C. to 11° C. the form and size were totally unaltered, and the number of eggs only one to two; no growth stages and no young brood were observed.

Then suddenly by $^{5}/_{V}$ at a temperature of $+12^{\circ}$ C. the alteration began. We then met with large females the size of which was about 11—1200 (Fig. 30a). They were typical roundheads or with slightly pointed heads. The number of eggs was augmented to about 5. These females were present the whole of May increasing in size to about 1500, the whole augmentation falling only upon V. The size of A was almost unaltered, only about 140—120, and A + B therefore only below or about $^{1}/_{2}$ V. In the last part of the month fertility was considerable, 12—15 eggs. The forms were extremely clumsy (about 800, Fig. 32a). Simultaneously growth stages appeared, at the beginning of the month only in small numbers but almost suddenly, on $^{24}/_{V}$, numerous. These growth stages had all pointed heads with T = about 1000 (Fig. 32c). A was now about 250—280 and A + B $>^{2}/_{3}$ V. At this size maturity was reached. Simultaneously young brood, always with pointed heads, and with A about 134 and A + B $>^{2}/_{3}$ V, appeared.

This sudden appearance of a rather abundant amount of young brood and growth stages differing very much in size and form from the very few old clumsy females, can only be ascribed to the fact that now large amounts of ephippia were hatched.

By $^{16}/_{VI}$ the great variation had asserted itself; the big females with $h = 900$ had disappeared, the size was now only 1000 to 1100 (Fig. 33a), but A was now about 2—300 and $A + B$ about $= V$. The young brood began with $A = 252$ three times more even than in the old females from the winter generation.

D. cucullata in the lake of Frederiksborg castle presents no peculiar phenomena. The size is rather small, T being in summer 12—1400 in winter only about 1000, still it is not smaller than *D. cucullata* in Furesø where T is 1400 during summer and in winter 800—900. The periodicity is the same as in larger lakes, the maximum lies at the highest temperature in August—September; it was extremely common the whole autumn, and in the mild winter 1924—1925 to March 1925 it was quite exceptionally common. The number of eggs in the egg sets is normally highest in spring (12), very low during summer (4—1). It is of interest that it has now been shown that a slow parthenogenetic propagation really goes on regularly at a temperature of 0—3° C. during the whole winter, and that young brood, even if rare, is to be found. WAGLER (1923 p. 81) has supposed that the hibernation took place in larger lakes with deeper water strata, where the temperature is much above the temperature of the surface. With regard to the lake of Frederiksborg castle, with a depth of only above 3 m., this is not the case. It is further peculiar that the sexual period is so exceptionally pronounced that for the last 25 years it has every year been observed in October—November, and that its results, the ephippia, are present in huge masses during October—May. In lakes the species is mainly acyclic. It is in full accordance with what I have described in my Plancton Investigation (1908 p. 185—195) to which I therefore refer the reader. Most probably it is not possible to distinguish *D. cucullata* from the lake of Frederiksborg castle from that of Furesø (Plancton Investigations Tab. XX—XXI).

D. cucullata in Hestesko pond.

Tab. I.

Date	T	A	B	A + B	V	$\frac{A + B}{V}$	S	H	eggs	Fig.
1924 $^{25}/_5$	1176	168	168	336	840	$^{336}/_{840}$	420	588	6—7	1
$^{29}/_5$	1596	168	252	420	1176	$^{420}/_{1176}$	420	1008	30	2
$^{29}/_5$	1538	302	252	554	984	$^{554}/_{984}$	588	756	9	3
$^7/_6$	1848	252	252	504	1344	$^{504}/_{1344}$	420	840	11—12	4a
$^7/_6$	1260	336	168	504	756	$^{504}/_{756}$	454	504	3—4	4b
$^7/_6$	554	134	84	218	336	$^{218}/_{336}$	302	168		4c
$^{12}/_6$	1512	168	252	420	1092	$^{420}/_{1092}$	504	804	8—10	5a
$^{12}/_6$	1344	336	168	504	840	$^{504}/_{840}$	420	588	6—7	5b
$^{12}/_6$	1028	252	134	356	672	$^{356}/_{672}$	336	504	1	5c
$^{12}/_6$	924	252	168	420	504	$^{420}/_{504}$	336	336	1	5d
$^{12}/_6$	672	168	84	252	420	$^{252}/_{420}$	252	252	1	5e

Date	T	A	B	A + B	V	$\frac{A+B}{V}$	S	H	eggs	Fig.
12/6	554	134	84	218	336	$\frac{218}{336}$	302	168		5f
19/6	1378	252	202	454	924	$\frac{454}{924}$	252	756	6-7	6a
19/6	1028	168	168	336	672	$\frac{336}{672}$	252	504	2	6b
19/6	974	252	134	386	588	$\frac{386}{588}$	336	250	2	6c
19/6	520	134	84	218	302	$\frac{218}{302}$	336	168		6d
30/6	1428	252	252	504	924	$\frac{504}{924}$	504	739	4	7a
30/6	1512	420	252	672	840	$\frac{672}{840}$	386	588	2-3	7b
30/6	874	202	168	370	504	$\frac{370}{504}$	420	336	1	7c
30/6	554	84	168	252	302	$\frac{252}{302}$	286	168		7d
15/7	806	302	168	470	336	$\frac{470}{336}$	336	252	2	8a
15/7	772	134	134	268	504	$\frac{268}{504}$	336	336	1	8b
15/7	756	168	84	252	504	$\frac{252}{504}$	252	336	1	8c
15/7	504	84	84	168	336	$\frac{168}{336}$	252	168		8d
1/8	772	134	134	268	504	$\frac{268}{504}$	252	302	1	9a
1/8	547	161	84	245	302	$\frac{245}{302}$	302	268		9b
1/8	503	117	84	201	302	$\frac{201}{302}$	168	336		9c
15/8	840	84	168	252	588	$\frac{252}{588}$	302	386	1	10a
15/8	722	134	84	218	504	$\frac{218}{504}$	336	252	1	10b
15/8	504	84	84	168	336	$\frac{168}{336}$	252	336		10c
10/9	840	84	168	252	588	$\frac{252}{588}$	302	386	1	11a
10/9	726	168	134	302	504	$\frac{168}{504}$	302	336	1	11b
29/9	890	134	168	302	588	$\frac{252}{588}$	252	433	4-1	12
15/10	772	134	134	268	504	$\frac{268}{504}$	285	403	2	13
25/10	958	118	168	286	672	$\frac{268}{672}$	201	504	Ehip.	14
1/11	941	118	151	269	672	$\frac{269}{672}$	336	504	Ehip.	15
11/11	874	134	151	285	588	$\frac{285}{588}$	336	420	2	16
28/11	890	134	168	302	588	$\frac{302}{588}$	252	420	2	17
8/12	874	118	168	286	588	$\frac{286}{588}$	252	504	1	18
8/12	874	118	168	282	588	$\frac{286}{588}$	252	588	Ehip.	19
28/12	806	84	134	218	588	$\frac{218}{588}$	285	454	2	20

D. cucullata. Primiparæ.

12/6	924	252	168	420	504	$\frac{420}{404}$	336	336	1	5a
19/6	974	252	134	368	588	$\frac{386}{588}$	336	336		6c
30/6	874	202	168	370	504	$\frac{370}{504}$	420	336	1	7c
15/7	772	134	134	268	504	$\frac{268}{504}$	336	336	1	8b
15/7	756	168	84	252	504	$\frac{252}{504}$	252	336	1	8c
1/8	772	134	134	268	504	$\frac{268}{504}$	252	302	1	9a
15/8	722	134	84	218	504	$\frac{218}{504}$	336	252	1	10b
10/9	726	168	134	302	504	$\frac{302}{504}$	302	336	1	11b

D. cucullata. Neonatæ.

12/6	520	184	84	268	252	$\frac{268}{252}$	252	168		
20/6	520	184	84	268	252	$\frac{268}{252}$	252	168		
30/6	520	184	84	268	252	$\frac{268}{252}$	252	168		
5/7	460	118	84	198	252	$\frac{198}{252}$	252	168		
1/8	450	118	84	198	252	$\frac{198}{252}$	250	168		

The pond was ice-covered from $1/XII$ 1923 to $19/IV$ 1924, in all 143 days. Samples were taken on $7/IV$, $10/V$ and $16/V$. In these samples only one single specimen was found. As it was badly preserved and not to be distinguished from a young *D. longispina*, it was not drawn. —

On $25/V$ 1924 three specimens were found. T was 1150—1170. $A + B < 1/2 V$. (Fig. 1). A was 168. The number of eggs was 6—7. One of the specimens was round-headed, the others had a slight crest. During the time $29/V$ — $7/VI$ three samples were taken, 5—6 individuals were found in each of them. During this time the size increased much. T was 15—1800 but the whole increase was confined almost entirely to the valves, which reached 12—1300 (Fig. 2—3). A was only 170—250 and $A + B$ hardly more than $1/5 V$. Most of them were typical roundheads; they were very clumsy with $H = 840$. Number of eggs 6—8. The spina only about $1/2 V$. These very clumsy forms were found again in small numbers by $7/VI$; a single one (Fig. 4) on $12/VI$, Fig. 5 a. Then they totally disappeared. A few young ones, very slender with remarkably high crests ($A + B > 2/3 V$) were found. But these forms had not begun egg production. The species was extremely rare. In the broodroom of the clumsy roundheaded females were found high-crested young ones with $A + B = 3/4 V$ (Fig. 25). During the time $7/VI$ to $30/VI$ (4 samples) the number increased and in the last sample *D. cucullata* was rather common.

The size now only rarely exceeded 1100. In these larger forms (Fig. 6 a, Fig. 7 a) $A + B$ was 420—450 and $< 1/2 V$, often only about $1/3 V$. The animals had pointed crests with a convex ventral contour. A was about 250; they produced 6—7 eggs. These relatively large forms (Fig. 10 a) were rare. In the main forms (Fig. 5 c, Fig. 11 a) T was only 900—1000. $A + B$ was now about 500 $\bar{\bar{}} 1/2 V$ and A about 330. They produced only 1—2 eggs. They may be regarded as primiparæ. Especially on $19/VI$ there were a good deal of growth stages of a size of 550—700. $A + B$ only reached about 336, being commonly only $1/2 V$. On $13/VI$ a single specimen was found where $A + B$ was $> 1/2 V$. On $30/VI$ a few animals which had not begun egg production were found. $A + B > 2/3 V$. The propagation began with the size about 900; in these small females the number of eggs was only one; at 1000—1100 it reached 3—4 but was not higher. —

From the first part of July the very peculiar fact occurred that *D. cucullata* almost disappeared from the plankton in the course of a fortnight. From the time $15/VII$ 24 to $26/II$ 25 I possess 22 samples taken at regular intervals of about 10 days. The samples were taken with Gauze 20 and with Griesg. 60 which fishes *Asplanchna* very well. In most of the samples I was only able to get very few, often only 2—5 individuals. From $17/XII$ not a single one was observed. No sexual period was present in June—July.

What is still more peculiar is that from $1/VII$ the size decreased in a very strange manner, and during the rest of the year, even if it increased a little, was almost constant. T was only about 800 or even below. In these exceedingly small females $A + B$ was $> 1/2 V$ and A only about 90. They all produced only one single

egg. During the time September—December the size slowly increased to about 850—900, very rarely more. The number of eggs was never more than one or two. In this size the individuals carried ephippia during the period $^{25}/X$ — $^{28}/XI$. The increase during the whole period from $^{15}/VII$ to $^{28}/XII$ was almost entirely in the valves which increased slowly from about 680 to about 600—670. $A + B$ might reach 300 and A 100—130, rarely 160. During the whole period the ratio $\frac{A + B}{V}$ was almost unaltered. $A + B < \frac{1}{2} V$, commonly only near $\frac{1}{3} V$; the contour of the head was rounded with a slightly pronounced obtuse point; the ventral contour of the head a little convex; the spine commonly $\frac{2}{3}$ of the length of the valves. — The last specimens seen on $^{28}/XII$ did not differ from those from the foregoing samples.

— As far as I know, a dwarf race of *D. cucullata* from a small pond has hitherto never been followed regularly a whole year round. It may further be added that the exploration is also based upon a series of samples belonging to the year 1923; the main results from this year fully coincide with the results from 1924.

Now it will be clearly understood that there is really a very conspicuous difference both with regard to cycle as to cyclomorphose between this dwarf race and all races from lakes.

Just at the time, in the middle of July, when the lake races get their highest maxima and the waters teem with all stages of high-crested individuals, the pond race practically disappears; only a more thorough exploration will procure about 10 specimens in a sample, in many of them much fewer.

Just at the time when the lake races develop their strongest cristæ with $A + B =$ or often $> V$, A decreases in the pond race and $A + B$ is for the rest of the year only $< \frac{1}{2} V$ and often only near $\frac{1}{3} V$; the strongly pointed heads disappear, and already in August forms occur which are typical roundheads. Whereas A in the ponds in July and later on does not reach more than about 150, in lakes it reaches 700. The most remarkable fact now is that in the broodroom of these pond-roundheads of early autumn young ones are found with $A + B = \frac{2}{3} V$. But these young ones have not been found in the waterlayers; the few observed young ones have all had $A + B < \frac{1}{2} V$. It seems as if the young animals during the moults constantly increase the valves at the expense of the crista. —

A comparison of the neonatæ (Fig. 3) of the lake races with those of the pond races shows that the cyclomorphose begins almost simultaneously for both races (in May). At this time we find, both in lakes and in ponds, roundheaded, big mothers with high-crested young ones in the broodroom. When born, in both cases A is about 90—100; and during May—June A is augmented to 252 or more than double that and $A + B = V$ when the animal is born; whereas this is unaltered for the lake races during the whole of July and August, in the pond races already on $^5/VII$ A goes down to about 80, and $A + B$ is only $\bar{>} \frac{1}{2} V$. This ratio is unaltered during the rest of the year. In the lake races we do not meet with this ratio until about $^{15}/IX$.

Moreover, whereas in lakes the water from summer to October teems with newly hatched brood with $A + B = V$, in ponds the brood is almost absent, and only a very few specimens have been observed. —

With regard to the growth stages we find very peculiar relations. Egg production begins in both localities in May—June. T is about 1000, perhaps a little smaller in the pond. Whereas the primiparæ of the lake of Frederiksborg castle have $A + B = V$ and A 400—500 during the whole time from the middle of June to the middle of September, those of Hestesko pond have never $A + B = V$, only a

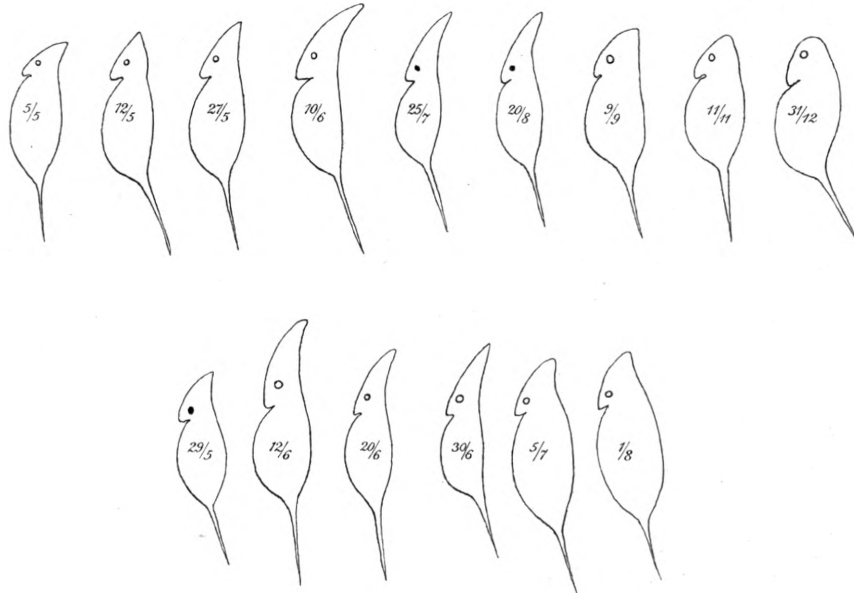


Fig. 3.

D. cucullata. Neonatæ from the lake of Frederiksborg castle (upper series) and from Hestesko pond (lower series). It will be seen that the Neonatæ from Hestesko pond already on $5/VII$, at the time when the cristæ in the lake of Frederiksborg castle are at their highest, are reduced to half their size and that the high cristæ from the first-named locality are preserved at all events 6 weeks longer than in the last-named one; further that brood in the Hestesko pond totally disappeared already in August. $30\times$

little more than $\frac{1}{2} V$ and A only 130—160. This means, in other words, that whereas A, in the lake races, is augmented by about 300 during growth, it is only augmented by about 30—60 in the Hestesko pond. Now it seems as if we are entitled to conclude that one of two things occur. In lakes there must be present a factor forcing the brood to augment A during growth. In the ponds there must be a factor which either prevents the development of A or causes the development of A to be unnecessary during growth. We further find that, whereas in the lakes the waters teem with neonatæ and growth stages during the whole time from the last part of June to late in December, already in July neonatæ and growth stages in ponds are extremely rare, and from August to December so extremely rare that it may be supposed that the propagation here has almost stopped.

When further we now compare the old animals in lakes and in ponds, even more conspicuous differences will be observed. —

In the lake the primiparæ and terminales augment T during the whole time from the last part of June to the first part of September; T is augmented during growth from 1000 to about 1500. In the pond this is only the case in June. From the beginning of July to December any augmentation of T is only with difficulty detectable and does not exceed about 100. The augmentation in size of the lake forms is mainly due to augmentation as well of A as of V, and that in the way that both are augmented equally; the ratio $\frac{A+B}{V}$ is commonly $\bar{=}$ 1. In the pond race $\frac{A+B}{V}$ is commonly only $\frac{1}{2}$ or rarely $\frac{2}{3}$ V. The augmentation of T is mainly due to the augmentation of V, and from the middle of July this is exclusively the case. The result is that in these old females $A+B < \frac{1}{2} V$, a ratio which is not met with in lakes until the last part of October—November i. e. $3\frac{1}{2}$ months later. —

Simultaneously we see that whereas the summer forms of the lakes are slender even as old animals, in the ponds they get big and clumsy; this begins here already in August and remains unaltered during the whole of the autumn. Curiously enough, in lakes and in ponds the summer forms only rarely produce more than one or two eggs, but whereas this is enough for the development of even enormous summer maxima in lakes, this is quite insufficient in ponds where a very conspicuous minimum occurs already in July just at the time when the maximum begins to develop in lakes.

As far as I can see, this can only be interpreted to mean that in the lakes very many small broods very quickly follow each other, whereas in ponds a factor must occur which tends to retard the development and produces the pronounced minimum. Both in the lake of Frederiksborg castle and in the pond a sexual period occurs; it comes simultaneously in both localities, in October—November. In both cases the species is monocyclic. —

From the foregoing we can presumably see in what manner the great variation in the behaviour, morphologically and biologically, of the lake and the pond race asserts itself. But the deeper cause of all this, why the young ones in ponds are suddenly in July born with an A half as long as a fortnight earlier, why suddenly A is not developed during growth, whereas it was so in June, and why T is not augmented after egg production whereas it was so in June, and why the propagation suddenly goes down in July, whereas it produces the large maxima in lakes with almost the same egg numbers, are all questions to which it is very difficult to find any answer. It is almost impossible to suppose that the primus motor should be the temperature; it may for a few days perhaps be $1-2^{\circ}$ Celsius more in the Hestesko pond than in the lake of Frederiksborg castle. In both water masses Clathrocystis begin huge maxima almost at the same time, in the Hestesko pond a little more than a week before. The lake as well as the pond are both overfilled

with organic matter; the pond unquestionably most. That the dwarf race should be a result of starvation is highly improbable. On the other hand, it seems most reasonable to suppose that there must in some way be something with regard to the assimilation which may in some way cause both the decrease in the length of A just at the time when it is augmented in the lakes, the decrease in the total length, and the slow propagation which causes the minimum just at the time when the maximum sets in in the lakes.

In 1924 the exploration could not be carried out on the above-named point and with the greatest interest I looked forward to the next year. It was my intention to carry the dwarf race from May into large cemented aquaria with water from the lake of Frederiksborg castle and then see if it was possible to augment the size of T and A and further produce a more fertile race. —

In contrast to the winter of 1923—1924, in which the pond was frozen for 143 days, the winter of 1924—1925 was extremely mild. The pond was open almost the whole winter. It might be half frozen over only for about 10 days in March. Samples were taken regularly during winter, but not a single individual could be found. When spring came samples were taken every tenth day; the very large samples were taken with the same net as in 1924, and every sample was examined for more than an hour.

During the whole year not a single *D. cucullata* occurred. On the other hand *D. longispina* had a huge maximum during summer with two pronounced sexual periods, and moreover, *D. pulex* appeared suddenly in the plancton. Simultaneously the *Daphnella*, which were rather common in 1924, decreased very much and disappeared totally already in August. In contrast to 1924 the summer of 1925 was extremely warm, and, as in many other ponds, the water volumes diminished considerably; the depth was lowered from 1 m. to $\frac{1}{2}$ m. That this diminution in water masses may in some way have influenced the development, especially of those species which mainly belong to lakes, is probable, but a more exact explanation of how this factor really asserts itself I do not know. Most probably gasses originating from the decaying bottom and causing the water in 1925 to be greyish and with a bad odour, have influenced these lake species, whereas these bad life conditions have been quite suitable for *D. longispina* and especially for *D. pulex*.

It is of the greatest interest that in two localities, the very small Hestesko pond and the lake of Frederiksborg castle, we have found two races removed from each other only by a distance of not $\frac{1}{2}$ kilom. which differ so much from each other with regard to life, life cycle, and cyclomorphose. In the pond the winter generation hibernates only as ephippium, in the lake both as ephippium and as a freeswimming organism. During summer the pond race has its minimum when the lake race has its maximum; further, in the pond race the cyclomorphose is depressed when it is at its highest in the lake race.

Most probably when this dwarf race was found in the Hestesko pond, dwarf-races had not been observed at that time; later on dwarf races of *D. cucullata* have

been found several times and are best studied by WAGLER who is also the only one who has tried to understand their occurrence. —

He has pointed out that *D. cucullata* may occur in very small ponds, of only 0.70 ha., nay even 0.15 ha.; he supposed that the main condition is not the size of the pond, and that there is a central part quite free from surface vegetations, but that the depth is not too small. Nevertheless, the depth may be very small; at all events in Hestesko pond it is never more than 1 m.; but in the summer of 1925, when the depth went down to about $\frac{1}{2}$ m., the *D. cucullata* did in fact disappear. WOLTERECK as well as WAGLER have observed that the species in these small ponds has no cyclomorphose at all; this can not be said with regard to the Hestesko pond. The strange thing is that the cyclomorphose begins in quite an ordinary manner, but just at the time when it is at its highest in the lakes and larger ponds the cyclomorphose disappears again, and then we only find roundheads.

At first WAGLER supposed that in these small races he had to do with "Hemmungsrassen"; later on he came to the result that the phenomenon must be due to the fact that the small races are ripe at an earlier stage, one or two ecdysis earlier than the other races (1924 p. 296). This should again be caused by better nourishment in small ponds and high temperatures should carry the organisms forward at an earlier stage to the ripe stage than in larger ponds and in the lakes, where the amount of nourishment is smaller and the temperature not so high. He finds a proof of his supposition in the fact that the exephippia females are always larger than individuals belonging to the later generations, the size of which is almost the same the whole of the summer and only a little augmented when autumn with lower temperatures arrives. This picture, however, only holds good for the monocylic generations. In dicyclic colonies phenomena of depression always occur, and as dicyclic and polycyclic colonies always occur in ponds and commonly not in lakes, this very phenomenon should therefore, according to WAGLER, assist the development of the dwarf races which as stated above are just bound to the smallest ponds. Further, as the cristæ are largest in the largest races, and these races are present in the lakes, whereas the races without cristæ occur in the smaller ponds, we are entitled to suppose that if the size of the body is dependent on temperature and nourishment, this may also hold good for the size of the cristæ, so that the highest cristæ may be developed in localities where the temperature is but low and nourishment but small, i. e. in lakes, whereas the low cristæ occur where the temperature is high and the nourishment copious, i. e. in ponds; the combination: habitats with high temperature and copious nourishment and di- or polycyclic colonies causes small cristæ; habitats with little nourishment, low temperatures and mono- or acyclic colonies favours the development of the cristæ. — With this new and at the first glance very seductive picture as his basis WAGLER now tries to give a new explanation of the cyclomorphose. We will here only restrict ourselves to seeing if the picture here given may be transferred to the race in the Hestesko pond. As far as I can see, this is by no means feasible.

WAGLER (1924 p. 298) correctly says that his suppositions "steht den bisherigen Anschauungen und den Erfahrungen aus Kulturversuchen diametral gegenüber". As my own confidence in the results of all experimental work upon sexuality carried on in very small aquaria is likewise but small, I confess that this fact should in my view not necessarily be a hindrance to the correctness of WAGLER's view. The worst is that his view is in the greatest possible contradiction to the results of so many facts brought forward by planctology during the last twenty years, so that it seems almost impossible that his views can be right. —

WAGLER maintains that the better nourishment and higher temperatures in ponds should cause the occurrence of dwarf races, because the ripe stages are reached at an earlier stage, i. e. at a lower size. At all events this is not the case in my localities.

In Hesteko pond as well as in the lake of Frederiksborg castle and in Furesø maturity is reached at the same size $V =$ about 500—600; during winter T is always the same, about 1000, but during summer, owing to the difference in the height of A in the primiparæ, it is in Hesteko pond about 900—1000, in the lake of Frederiksborg castle and in Furesø, about 11—1200.

Moreover, even if maturity were really reached at an earlier stage and in a smaller size in small ponds, nevertheless the question remains why the growth ceases in the ponds after maturity, whilst it continues in larger lakes during the whole summer season. Why is T in Hesteko pond never above 800 and V only 580 after June, whereas in the lake of Frederiksborg castle and Furesø T is 13—1500 and V 7—900? Why is the size of the primiparæ and the old barren animals the same in the small ponds, whereas in lakes V is about $\frac{1}{3}$ larger in the last-named animals than in the primiparæ? Of this fact which in my opinion is indisputable as well as being the main point in the whole question, WAGLER gives no explanation at all. —

When further WAGLER maintains that the dwarf races are a result of di- or polycyclic propagation, in my locality this also by no means holds good. In the Hesteko pond the sexual propagation year by year has always been very restricted, always bound to the autumn, the species is typically monocyclic; the same is the case with the species in the lake of Frederiksborg castle which, owing to its small depth, only about 3 m., is really only a pond, merely somewhat larger than Hesteko pond. The propagation in these two ponds is the same, but in one pond we find dwarf races, in the other not; it is, for my localities, impossible to imagine how differences in propagation should be able to explain the differences in size in the two races. —

When further WAGLER maintains that the exephippia females are always the largest, my experience shows that this is not correct. The very large females which we almost everywhere find in early spring at a temperature of only 5—10° C. are in my opinion not exephippia females, but are those individuals which have hibernated and now begin egg production with very high eggsets in early spring; they appear before the ephippia are hatched, at all events before the exephippia females

through a series of ecdyses can have reached the large size; furthermore they are normal in typically acyclic colonies. If, however, it is impossible to combine small size with copious nourishment and high temperatures, it is also evident, that the disappearance of cristæ in small ponds cannot be traced back to the same phenomenon.

WAGLER (1924, p. 300), however, calls attention to another fact which is perhaps of much greater significance. As well known, the thermocline in lakes and ponds of middle depth and with a broad beach lies deeper than in the large lakes with steep beach; the strata in which organisms demanding a high summer temperatures can live are therefore larger in ponds and smaller lakes than in the larger lakes. The danger of sinking downwards into the dark, cold, hypolimnium is larger in the lakes than in the ponds. In accordance herewith, in the large lakes the Daphnids try to accommodate themselves by means of extremely high cristæ by means of which the swimming courses should be more flattened than in smaller lakes where there is more latitude and where therefore the cristæ need not be so high. In ponds with a very slight depth the seasonal variation is totally abandoned because the water is homogeneously heated and the organisms therefore not threatened by any danger from an underlying colder zone. —

In reality the explanation is very fascinating and may actually be correct with regard to the very small ponds; with regard to the larger and smaller lakes it must be remembered that all the Danish lakes may really be regarded as large pond lakes all with sloping sides with the thermocline only lying at a depth of about 13—15 m. and all below a size of about 35—40 □km. In these lakes the cristæ are very long, and in reality not much longer than in our small very shallow pond lakes, like that of Frederiksborg castle, being only about 3 m.

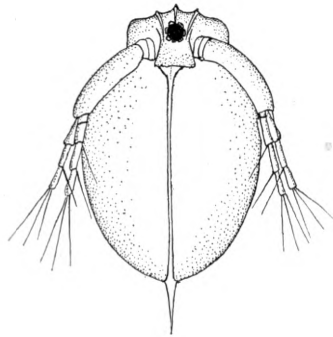


Fig. 4.

D. magna seen from below. 10×

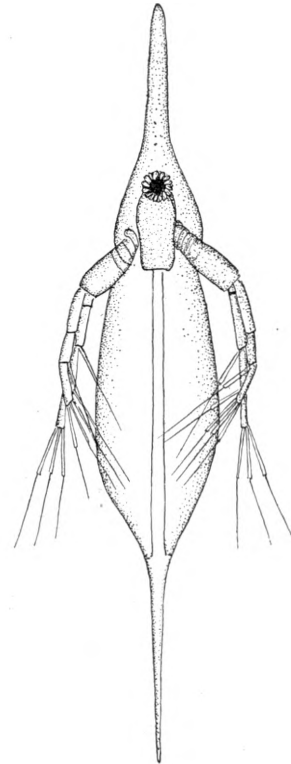


Fig. 5.

D. cucullata seen from below. 40×

The figures illustrate the transformation of the type when passing from littoral and pond life into pelagic life.

From the foregoing pages it will be clearly understood that in the species *D. magna*, *D. pulex*, *D. longispina*, *D. cucullata* we have to do with a series of forms which begins with *D. magna* living in the smallest possible pools and here partly as bottom forms in a manner nearly related to the life of certain members of the fam. *Estheridae*. The formseries finishes with *D. cucullata*, a true pelagic organism, whose

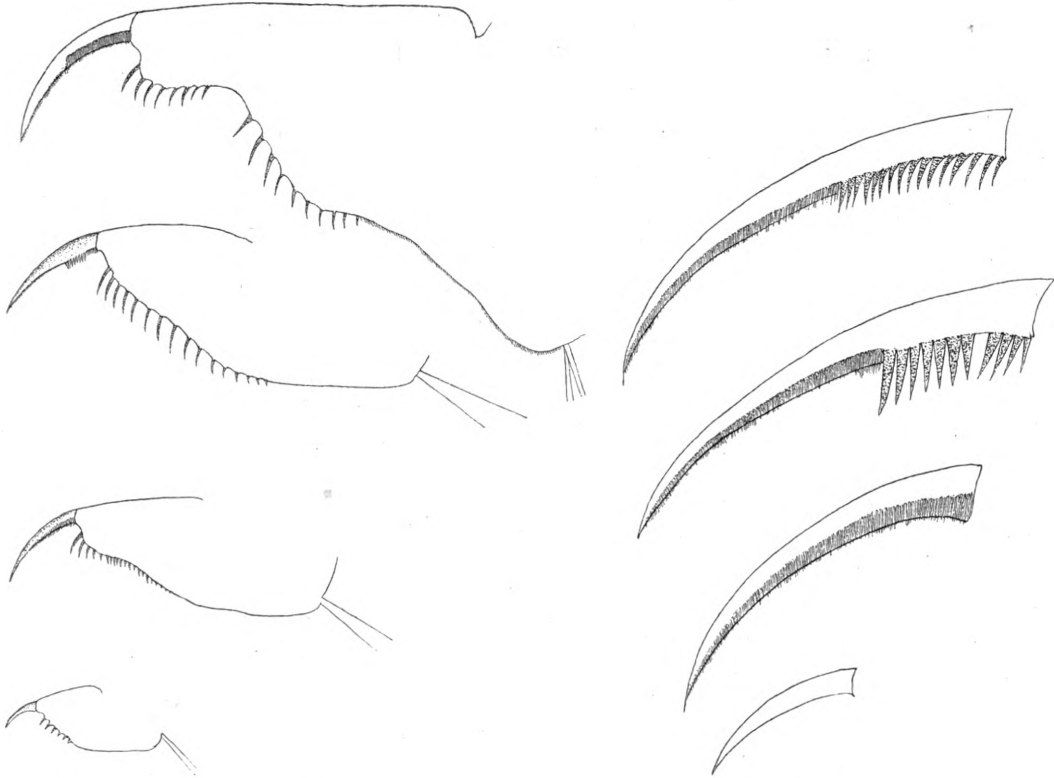


Fig. 6.

Abdomina of *D. magna*, *D. pulex*, *D. longispina*,
cucullata. 80×

Fig. 7.

Claws of *D. magna*, *D. pulex*, *D. longispina*,
cucullata. 250×

home is to be found in the pelagic region of our largest lakes. Especially *D. longispina* which can only with difficulty be distinguished from *D. pulex* is a species which has adapted itself to live under the most different life conditions.

The more the type accustoms itself to life under pelagic life conditions, the more the clumsy form of the body is altered into an elegant slender one (Fig. 4—5), the more the spinocity of the tail is reduced (Fig. 6), and the strength of the claws and their equipment with spines is reduced (Fig. 7); also the development of the fornices is reduced and so also is the system of the crossing ridges of the valves; the pigment spot is reduced and disappears totally in *D. cucullata*. Furthermore (Fig. 8) the size is reduced; the Neonat of *D. cucullata* is smaller than that of *D. magna* and

during growth the augmentation in size is but slight; as Primipar the *D. cucullata* is only half as long as *D. magna* and the height is only $\frac{1}{4}$. The number of eggs is in *D. cucullata* as Primipar one to two, in *D. magna* 10—12. During the development to pelagic life the eye gets smaller, but the lenses are more prominent; the first pair of antennæ are removed from the ventral contour of the head to the apex of the rostrum; the strength and, as far as I can see, also the length of the second pair of antennæ is reduced. We lack a more thorough exploration of the legs of the *Daphnia* species; I suppose that such an exploration would show a stronger development of bristles in the pelagic forms and species than in the littoral ones. —

The tendency to form-variation especially seasonal variation increases with the tendency to pelagic life; what begins in some of the pelagic races of *D. longispina* is accomplished in *D. cucullata*. The tendency to pelagic life causes the disappearance of the polycyclic; in *D. longispina* some of the races are dicyclic, commonly they are monocyclic and acyclic races may occur; in the pelagic region of the smaller lakes *D. cucullata* is commonly monocyclic, but in the larger ones very often acyclic.

Between the three species *D. pulex*, *D. longispina* and *D. cucullata* all transitional stages, morphologically as well as biologically, are to be found; but nevertheless their specific range may be regarded as indisputable. —

D. K. D. Vidensk. Selsk. Skr., naturv. og mathem. Afd., 8. Række, XI.2.

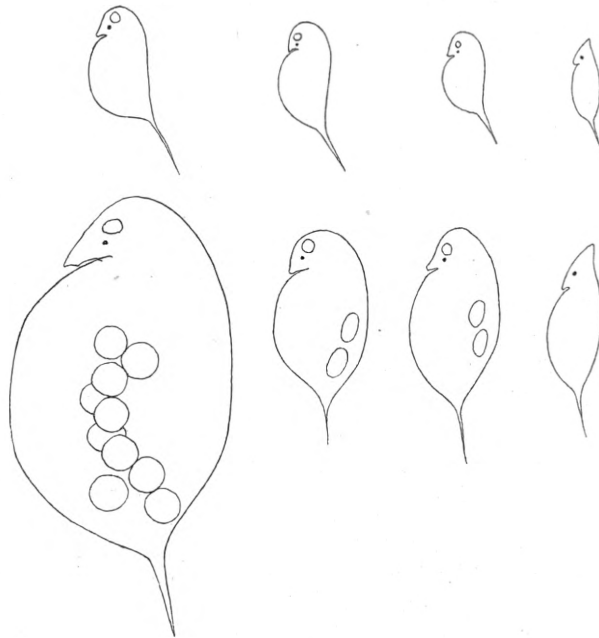


Fig. 8.

Neonatæ of *D. magna*, *D. pulex*, *D. longispina* and *D. cucullata* (upper row). 25×

Primiparæ of *D. magna*, *D. pulex*, *D. longispina* and *D. cucullata* (lower row). 25×

Parthenogenetic females from four different localities have been put in vessels of the same size and held at the same temperature and same amounts of nourishment. During the time $\frac{3}{5}$ — $\frac{4}{5}$ all produced neonatæ which were put in special vessels all of the same size and held at the same temperature and nourishment. During the time $\frac{18}{5}$ — $\frac{15}{5}$ the first eggs appeared, and the animals altered in primiparæ.

The neonatæ of *D. magna* is about 0.7600μ , that of *D. cucullata* only 0.200 , i. e. about 3.5 times smaller. The primiparæ of *D. magna* is 2270μ , that of *D. cucullata* 0.500 ; i. e. during growth *D. magna* has augmented its length more than three times, *D. cucullata* only about $2\frac{1}{2}$ times. Further that whereas H in *D. magna* is augmented from 0.400 to 1400 , i. e. about $3\frac{1}{2}$ times, it is in *D. cucullata* augmented only from 0.200 to 0.400 , i. e. about two times.

During accommodation to pelagic life the type is much reduced in size already from birth, it grows slowly during the moults and reaches maturity at a size much smaller than the offsprings type *D. magna*. Simultaneously the fertility is very strongly reduced, from 10—12 eggs to two or only one.

The formseries is an admirable example of the manner in which a type is altered morphologically and biologically in accordance with alterations in life conditions. —

Theoretical remarks.

a: The buoyancy theory.

Already in the last part of the foregoing century it was clear to many investigators that the fresh-water plancton organisms were subject to great variations. In a family or genus which contained as well littoral as pelagic species the range of variation was almost always greatest in the last-named species. That with regard to many species we could distinguish sharply between a local and a seasonal variation was only understood by a few; for several forms the local variation was fairly well known; that a regular seasonal variation existed was only pointed out for a single type: the plancton daphnids, and in reality only for one single species, now commonly determined as *D. cucullata*. A more thorough historical sketch having been given, it may now be regarded as unnecessary.

After ten years' study (1898—1908) of the plancton in nine of our Danish lakes the following facts were stated as the main results.

1. A long series of plancton organisms systematically belonging to very different parts of the animal and vegetable kingdom are subject to a very conspicuous local variation.

2. Many of these different organisms are also subject to a still more pronounced seasonal variation.

3. The seasonal variation may in the same species show a conspicuous local variation so that it takes a very different course in the different lakes.

4. The seasonal variation is most strongly developed in the perennial forms, not or only to a slight degree in the pronounced summer forms which appear in May and disappear in October.

5. In these perennial forms seasonal and local variation are almost only pronounced during the summer season from about 15 April to the 15 October. At temperatures near zero no seasonal variation is present; furthermore, there is also no local variation. The colonies from different lakes resemble each other very much during winter, commonly so much that they cannot be distinguished from each other.

6. The seasonal variations do not begin gradually through a series of even transitional stages; they are completed in the course of a very short time ca. two or three weeks, i. e. at a temperature of 12—16° C. (at the end of May and the beginning of June). In this relatively very short time Diatoms change their shape of colony, in *Ceratium hirundinella* the fourth horn is developed, or new, narrower and longer seasonal forms are observed, the longitudinal axis in *Asplanchna* increases in certain localities, the series of variations in *Synchaeta* and *Anuraea* arise, the growth in the tip of the crest in *D. longispina* and *D. cucullata* proceeds, the hunch in *Bosmina coregoni* grows upward, and the first pair of antennæ grow in length; *B. longirostris* as well as many other of the above-named forms decrease in size. —

7. At the same time as the seasonal variation in the perennial forms sets in, the periodical summer forms with their highly developed floating apparatus (*Holopedium*, *Bythotrephes*, *Diaphanosoma*, *Leptodora*, many *Rotifera*, many small peculiar *Chlorophyceae*, and other organisms characterised by gelatinous envelopments, extreme elongation of the longitudinal axis, etc.) appear. The result is, before summer, a plancton community with quite another appearance than that which was to

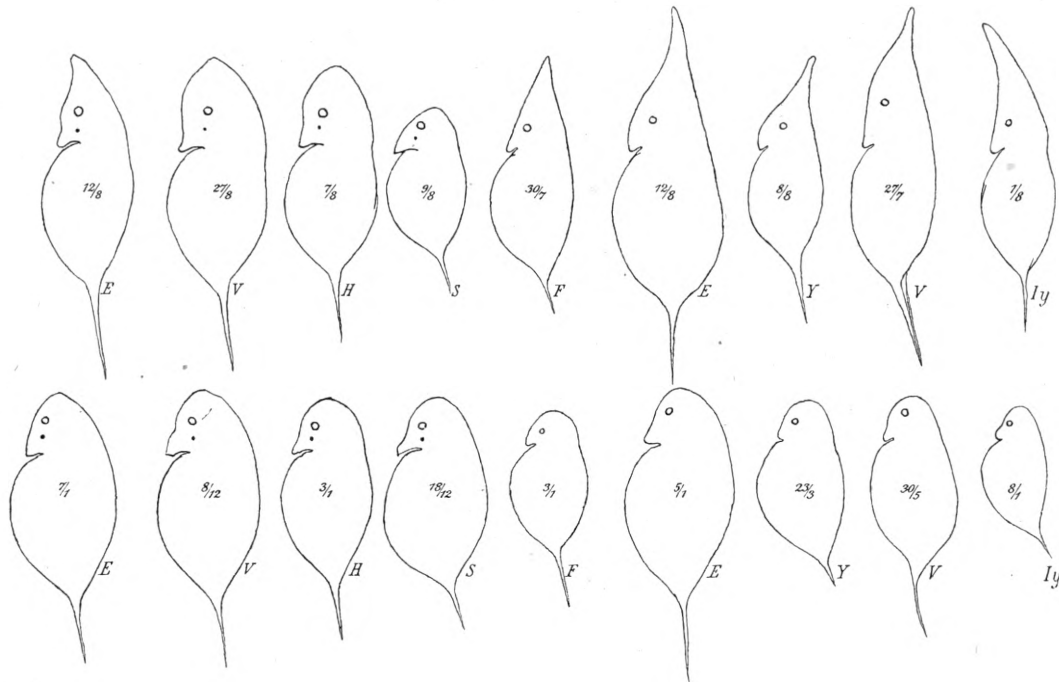


Fig. 9. Summer races and Winter races of *D. longispina* and *D. cucullata* from Danish Lakes. 30×
Upper row: Summer races, lower row: Winter races.

E, V, H subsp. *D. longispina* from Esrom lake, Viborg lake og Hald lake, S subsp. *D. hyalina* from Sorø lake; F, E, Y, V and Iy *D. cucullata* from Fure lake, Esrom lake, Hald lake, Viborg lake and Juul lake.

During winter not even the species can always be distinguished from each other.

be found during winter and in early spring. However far the local variation is carried, however peculiar the seasonal variations are, the races of the perennial species, wherever investigated, fall back in winter upon one and the same form, which in each species is invariably the same in all the localities investigated; when the seasonal variations begin again in the spring, and the local races assert themselves, they originate all from this common form. This common winter form is the homogeneous element from which all summer races proceed and to which all return.

With regard to the Cladocera it could further be shown that the seasonal variations were chiefly connected with the occurrence of new broods in spring during the abrupt change in certain fixed generations. The chief adaptations take place during the embryonal development, so that the young ones, when hatched

have another appearance than the mother animals had when growing up. Furthermore it was shown that by a rather abrupt change the whole plancton community had, by a variation in form, got quite another appearance in June—July than in March—April. The plancton is more hyaline; many perennial organisms have got their longitudinal axis elongated; the newly hatched summer young of *D. longispina* and *D. cucullata* were born with A respectively 80 and 140—200 μ longer than in the winter forms: in the growth stages the cristæ grow faster than in the growth stages of earlier generations, and even after maturity the cristæ may be further augmented; some plancton organisms living in colonies change the form of their colonies; the length of thorns are in some cases augmented, simultaneously with that appear of organisms with large gelatinous envelopes, and extremely elongated longitudinal axes or highly remarkable thorns.

8. After these structural characters have once been completely formed, during the above-mentioned abrupt change, their form is not appreciably altered in the course of the summer.

The appearance which the individuals of the species present in June is on the whole the same, also when the temperature of the water is at its highest; still some augmentation may commonly be shown.

Sooner or later after the temperature of the water has passed the highest point some of the above-named structural characters in the perennial forms are again reduced, and simultaneously the periodical plancton organisms disappear.

9. The sudden and contemporaneous occurrence of the seasonal variations during the great abrupt change in spring has no parallel in autumn when the structural characters characterising the summer plancton are again drawn in. With regard to the Cladocera it could further be observed that the rate of development of the form-changing power was dependent on the rate at which the moults take place.

In spring the new series of generations develop under continually and very rapidly rising temperatures, in autumn under continually and slowly falling temperatures.

When the reduction of the floating apparatus goes on so slowly in autumn, it is connected with the fact that the moults decrease in number and intensity; the number of times that external conditions can have some shape-forming influence steadily decreases.

The whole peculiar phenomenon, that the entire plancton alters its form, very suddenly in spring and only slowly in autumn, was in my opinion connected with the fact that the development of the structures brought about by the seasonal variations is to a much higher degree a *conditio sine qua non* than their reduction. But the main cause of the phenomenon: why the plancton community in toto was subject to this great regular seasonal form-variation unknown in any other community, also in the plancton community of the sea, was for years a matter of observation and speculation.

10. It could only be pointed out that if a long series of organisms belonging to a community year after year at the same time altered its form, a phenomenon to

which we have no parallel in other communities, we were forced to suppose that there existed in the freshwater a mysterious factor which, so to speak, compelled the periodical freshwater planctons to alter their form in spring, and again in autumn to revert to forms which we were customarily inclined to regard as normal. This was supported by the fact that, at the same time as the perennial planctons began their seasonal variation, at the highest temperatures of the water forms appeared which differed very much from all their nearest relations, and all possessed a very peculiar aspect. —

11. In discussing the local and seasonal variations of the plancton organisms it must be remembered that in all the cases where we have to do with sex material, and where there is a distinct difference between the two sexes, the variation as far as I know mainly affects the one sex. Restriction of variation to the female sex as well in Cladocera as in Rotifera is, though natural, of no slight importance.

12. About 1890 it was shown, especially through the study of marine planctons, that the plancton organisms present a considerable series of structures in common, viz. long thorns, plate-shaped expansions, jelly membranes, etc., which were all supposed in some way to counteract the falling velocity, and thus because they helped the organisms to sink slower, so to speak acted as buoyancy-organs; by means of them the cross section resistance was augmented, and the muscle power which the organisms were to use to counteract the fall could be reduced.

The seasonal variations of the perennial plancton organisms were (W.-L. 1900) regarded from the same point of view, and it was emphasised that the peculiar aspect of the periodic summer forms was due just to a peculiar hypotrophic development of structures which could be regarded from the same point of view (*Lep- todora*, *Holopedium*, *Notholca longispina*, a. o.).

13. The result therefore seemed to be that on the whole we were induced to suppose that the summer plancton in a lake in our latitudes would possess a much smaller falling velocity, i. e. a much greater floating capacity, than the winter plancton. — Already in 1900 (p. 650) it was shown that the quantity of dead plancton which has, during summer, three or four weeks earlier, lived in the upper layers and had been replaced by another plancton, could now be found as empty skeletons or chitine in deeper layers below the thermocline. It was therefore concluded that the deeper water layers on the whole offered bad life conditions for the plancton organisms and were in many cases only able to bring death to them. It was for this reason emphasised that the main conditions for the continued existence of plancton is the ability at all events during summer to remain above those water layers in which they would perish (1908 p. 15).

14. Excluding the surface layers with their extreme conditions of light and motion, the midmost water layers were regarded as the home of the freshwater plancton (W.-L. 1908 p. 15).

Further, if the freshwater plancton was living in a medium where the conditions for remaining above those water layers in which they would perish were

subject to regular seasonal variations, and the variations were of a dangerous kind, the plancton organisms had only one of two things to do (1.) to sink down into layers, in which they could not commonly live or (2.) in some way to alter their floating or swimming power. Now the result of the explorations was (1.) that very many periodical plancton organisms were really subject to seasonal variations and moreover (2.) that most of all these seasonal variations kept time with each other, at all events they reached their highest development at the highest temperature; lastly (3.) that all seasonal variations seemed strongly to develop just those structures which are customarily regarded in the marine plancton as means by which they increase their floating power. From these observations it was concluded that the rate of sinking was really subject to regular seasonal variation, and that the seasonal variations of the freshwater plancton organisms were the actual consequence hereof. The explanation of the seasonal variation of the plancton organisms (1900 p. 606) was found in the variation in specific gravity resulting from the regular seasonal variations in the temperature of the freshwater. Almost simultaneously (1902 p. 596) OSTWALD sought the explanation also in the regular changes in the physical and chemical nature of the surrounding medium; contrary to myself he supposed he had found it in the regular seasonal variations of the viscosity; since the variations in specific gravity, even if not proportional, still follow those of the viscosity, OSTWALD'S hypothesis was perhaps more correct than mine, but not, at any rate, contradictory to it. The result was therefore that in the following years the explanation of the seasonal variation of the plancton organisms as a result of the seasonal variation in the specific gravity and viscosity was called the buoyancy theory. —

15. With regard to some papers by the Swedish naturalist NAUMAN, which will be treated in the last part of this work, it is necessary to point out that OSTWALD and I have used the term buoyancy in the way which was customary at that time even if, physically speaking, it is not the most correct. As, however, we have both defined buoyancy organs as "organs which decrease the rate of sinking" (see e. g. W.-L. 1908 p. 5 and 15) and have again and again treated the seasonal variations as means by which the falling velocity, which is greater in summer than in winter, was counteracted, it will be understood that all these organs and seasonal variations have by no means been regarded as means by which the organisms were able to float in the water layers, but only as means by which they were able to keep in the right water layers and as means which reduced the muscle energy which must otherwise have been used. In this way almost all later scientists have used the word buoyancy. That real buoyancy organs (airbladders) which are well known in the marine plancton, apart from the *Corethra* larva, are unknown in the freshwater plancton, is a fact so well known that any special remark upon that point seems superfluous. It is only on account of some papers by NAUMANN (1924 No. 26 p. 2 and No. 24 p. 3) in which it seems as if NAUMANN supposes that the conception of buoyancy organs in this way is something new that it is necessary

to call attention to this fact. — In this work the terms buoyancy and buoyancy organs are used in the same way as in 1908.

16. For a time I supposed that the seasonal variations were due to variations in nourishment, but this supposition I soon abandoned because in my opinion these variations never were or could be of such a regularity that they could create this almost incredible harmony in the course of the seasonal variation, not only in the same lake from year to year, but in all the Baltic lakes in which explorations were carried on. And, more than that, that they could influence a long series of plancton organisms in the same manner and, so to speak, slowly force them towards the same goal, make them keep time with each other in their efforts, make them reach the goal almost simultaneously and then again, having driven them often to the extreme limits of their variations, slowly to make them go back to the starting point of all these variations. Variation in nourishment might be the agency by which all this was possible, but owing to irregularity in variation it could never be the *primus motor*, the driving force. —

The observations upon which the theory was built up were commonly accepted as established facts; in the first few years the theory, to use the words of C. SCHRÖTER, was regarded as “einer äusserst glücklichen Idee die uns einen ersten Hoffnungsschimmer auf einem kausalen Einblick in das noch so dunkle Gebiet der Planktonvariation giebt” (1901 p. 202).

Since 1905 an enormous literature relating to the freshwater plancton has appeared, and very many of these papers have adopted the theory. A series of observations were brought forward which did not seem to be in accordance with the theory. Most of this material came from scientists who had only observed the plancton in a single lake, very often only part of it, either the zoo- or the phyto-plancton, or very often only a special group of plancton organisms, often only a single one in a single lake. As far as known, nobody has followed the seasonal variations simultaneously throughout two years upon a series of plancton organisms in a series of lakes. Hence it is quite intelligible that they have no understanding of that which is really the main point in the theory, viz. that the variations in the supporting power of the freshwater do not specially influence a few organisms e. g. *D. hyalina*, *D. cucullata*, a *Bosmina* a *Brachionus*, but that the total amount of freshwater plancton over wide areas of its distribution is subject to the very same sole law prevailing throughout. That this law itself is difficult to understand because it only seems to influence the life of this very community, must be admitted.

Moreover, it is very difficult to carry out simultaneously regular explorations in a series of larger lakes. The first condition is that the scientist lives in a district with larger lakes and, further, has a robust physique and unlimited time at his disposal. It is therefore intelligible that the explorations were partly for that reason transferred from the lakes to the ponds in the following years. The buoyancy theories arose from studies in the lakes, but to a very great extent they were

tried on the basis of studies in ponds, often in ponds with a depth of not more than one meter. Moreover, as limnology was to be taken into the service of fishery, they were very often, especially during the last years, tried in artificial ponds with depths below one meter, and regularly emptied once or twice a year. —

The scientists — all young or very young men — seem to have lacked all understanding of the fact that the results, gained in localities of this nature, when regarded in the light of the buoyancy theory, must necessarily be used at all events with some reservation and some caution.

The worst of all was, however, that some of the freshwater planctons, especially the Cladocera and quite especially some *Daphnia*- and *Bosmina*-species, were made to serve as a support for the theories of heredity. The study of the freshwater plancton was to a very high degree transformed into a study in the laboratory. It must be admitted that limnology and also the buoyancy theory has in many respects derived great advantage from the removal from nature herself to the laboratory; on the other hand, in very many respects it has lost very much. This is mainly due to the fact that the observers have lost connection with living nature.

From different points of Europe ephippia have been sent to the laboratories, especially that of Leipzig; with only a very fugitive knowledge of the real life conditions, and almost always without regular fortnightly exploration of the habitat the material, hatched from the ephippia, has been studied in the aquaria, often in volumes of water of almost incredibly slight size (5—10 cm.). Varying the life conditions with regard to nourishment, temperature, viscosity, chemical composition of the water, and light, the experimenters seem to suppose that the fact that the organisms have been removed from water volumes commonly of many hundred cubic meters into water volumes of only 5—10 cm. has no importance at all with regard to the results. This is so much the more remarkable as WAGLER (1923—1924) has shown that life in very small shallow ponds in the case of *D. cucullata* produces special dwarf races without cyclomorphosis. All the innumerable sources of error with which exclusive laboratory work is always afflicted might have been much reduced if the explorations had been carried on simultaneously with outdoor studies. Especially the fact that these new plancton investigations have been of such a pronounced laboratory character has brought about the result that the very plancton organism just studied has never been regarded as a member of the plancton community, but always merely "als Ding an sich". For that very reason the explorers seem always, in their studies and in their results, to have forgotten that just those seasonal variations which they are momentarily studying are not something peculiar to just that single organism, but are in accordance with seasonal variations in very many plancton organisms, and that all these seasonal variations follow parallel lines, begin in the course of a fortnight in nature, reach their highest development at temperatures nearest the highest which the waters can produce, and slowly diminish at falling temperatures. The conception of the seasonal varia-

tion of the plancton organisms was originally based upon the study of the entire plancton community; not one of my numerous critics have met me upon this ground; all experimental work has almost exclusively been carried on upon one single Cladocera, *D. cucullata*, a little upon *D. longispina* and very little upon *Rotifera* where the results are very contradictory.

All these objections made to the theory in its infancy were well known to myself. During my studies I had met with them all, but my standpoint was: not to regard the theory as wrong because they were not in accordance with it, but to study the matter again and see why the new facts could not be brought to agree with the theory.

I regarded it as a matter of course that, although the seasonal variations proceed on parallel lines in the different localities, considerable variations may nevertheless assert themselves. This holds good too with regard to details in the manner in which the organism meets the demands for variation. Like other living organisms, those of the plancton have more than one string to their bow. Because it would be most convenient for us, they do not consider themselves obliged to use the same string everywhere. Here is a point which, owing to the absence of observations in Nature herself, many of my critics have often overlooked. Although we will later on return to the following points, it may be permitted already now to remark that as early as 1908 (p. 252) it was shown that the buoyancy organs, even if they regularly were developed at the highest temperature, still often reached their highest development much later, viz. long after the highest temperatures were passed. This was to me a matter of course.

Furthermore (1908 p. 251) I regarded it as a matter of course that the total amount of individuals belonging to a species at a particular moment in a given locality does not show the new measures. Individuals will always remain which, in the development of their floating apparatus, may be regarded as retarded. Of *D. cucullata* low crested forms steadily decrease during summer, high crested steadily increase. With regard to *D. galeata* in Littois Träsk WAHLBERG (1913 p. 83) has arrived at quite the same result. Of course all low crested individuals do not die away on the same day, nor in the same week. Objections of this nature used as proofs against the buoyancy theory are always raised by scientists whose material of exploration has been the slightest possible.

Before entering in detail upon the criticism the following may still be added. For reasons set forth in 1908 (p. 313—314) I regarded the fresh water plancton among the oldest communities of the earth. In this manner, and not so much as other scientists suppose merely owing to passive migration, the cosmopolitanism of the society was interpreted. During the ice age the fresh water plancton was driven out of vast areas of its former distribution. The view that the collective fresh water plancton should have arisen under arctic conditions with their original home in arctic seas and in arctic fresh waters was vigorously opposed (1908 p. 336). When

the ice disappeared and the fresh water fauna again took possession of its old areas, the climate differed very much from that of previous days.

Owing to the fact that all explorations carried on in the far North seemed to show that seasonal variation, if present, was very feebly developed under arctic conditions, and local variation not so conspicuous as under milder climates, it was concluded that the deeper basis of the causal connection between the variations in the plancton organisms and those in the bearing power of fresh water was to be sought in the amelioration of the climatic conditions which began after the Glacial Age, the consequent higher temperature of the water, and at the same time the continually increasing rate of sinking.

Local and seasonal variation in the plancton are phenomena which have arisen during the melting period of the ice. They are to be considered as the reply of the organism, in part to the lack of uniformity produced by the milder climate and the greater differentiation in the outer conditions, in part to the greater demands owing to the rising temperature on the floating power of the species. The peculiar fact that, in the temperate zone, the plancton crustacea fall back during winter to forms which greatly resemble the form-fixed arctic races strongly corroborates this view; this return in winter to the arctic races is a feature in the development of the organisms which has been preserved from the temperature conditions of by-gone times. The development which the Crustacea undergo every year: the appearance in spring of the numerous races, the seasonal variation in these, the disappearance of the racial stamp during winter, and their return to the common form which is nearest related to the arctic and North-European forms in which seasonal variation is absent, is only a condensed summary of the development which the Crustacea have undergone from the melting period to our day. Later on this view was corroborated by others e. g. by BEHNING with regard to *Limnospiza frontosa* in the southern part of the Wolga (1913 p. 446).

It has been adopted by THALWITZ (1910 p. 38). RÜHE (1912 p. 123) says in his very valuable *Bosmina*-monograph: "Somit kan ich die Eiszeittheorie, obwohl ich geneigt bin, ihr — gegenüber die Einwanderungstheorie — die grössere Wahrscheinlichkeit zuzuschreiben, beim gegenwärtigen Stande unserer Kenntnisse nur den Werth einer Arbeitshypothese beanspruchen, die künftigen faunistischen Untersuchungen Ziel und Weg zu weisen geeignet sind."

As the variation of the plancton organisms becomes most conspicuous at a temperature above 12—16° C., and toward the north almost stops where the oak forests cease, we may believe that the turning point in the tendency to variation, that which corresponds to the great turning point in spring in our times, has taken place during the oak period, which may in so many respects be designated as the transformation period, the spring time in the developmental history of our country and its flora.

During immense spaces of time the pelagic region of the lakes was populated by organisms of which a smaller part originally belonged to the sea and slowly

adapted themselves to the life in fresh water, while a much greater part consisted of organisms which had quite another origin. The great bulk of all fresh water plancton may as mentioned in the introduction, be designated as bottom- and littoral forms which have adapted themselves more or less to pelagic life, and for a period of their life made themselves independent of the bottom and bank where the great majority still pass a shorter or longer period of their lives. Many of the plancton organisms may be arranged in developmental series beginning with clumsy littoral forms and ending in elegant hyaline plancton forms. Nowadays, as in the early epochs of our earth the pelagic region is and has been populated as well from the sea as from the shore; from both these areas the transformation goes on to this very day even though in different ways. As far as I know most scientists have shared this view. (KURZ 1913 p. 468 a. o.).

The occurrence of the numerous local races in the temperate zone is favoured by the frequent monogonic reproduction in plancton organisms (asexual formation of auxospores in Diatoms; hardly constant and regular conjugation, but mainly reproduction by partition in *Ceratium*; conspicuous tendency to acycly in Rotifera and Cladocera). Directions of variation once begun can therefore continue undisturbed; no crossing from conjugation and consequent disturbance and interruption in the directions of variation commenced take place. Resting-stages, resting-cysts, resting-eggs etc., which are as a rule also the means of the distribution of the species, are lost with the disappearance of digonic reproduction. In this way the races may be separated; each locality becomes an exclusive world to them. The explanation is, however, not quite satisfactory. (See later on).

When local variation has become very much reduced under arctic conditions and seasonal variation almost untraceable, I supposed this was due to the fact that sexual propagation here seems to play a much greater part in the cycles than in more southern latitudes; racial characters are obliterated by means of amphimixis; tendency to acyclie is augmented from north to south and through selection, owing to the higher rate of sinking for females carrying resting organs, almost obliterated in lake races.

Later on OLUFSEN'S explorations of the Cladocera of Spitzbergen (1918 p. 392) seemed to show that the supposition does not at all events apply to all members of the plancton community. As mentioned on p. 19 one of his main results is that under arctic conditions the ephippia are formed without foregoing impregnation. Whereas ephippia are formed in enormous quantities, and much more than in lower latitudes, he has never seen a male in the Arctic, and maintains that males of *Daphnia* have never been found in the Arctic, this phenomenon being due to the peculiar, very difficult life conditions. These results, based upon very important material, seem to reverse the theory assuming amphimixis to cause the common stamp of arctic races. This may, however, constantly be referred to the enormous production of resting eggs and the huge masses of birds which carry the ephippia from pool to pool.

Some observations seem to corroborate OLUFSEN's view. It has been shown by v. SCHARFFENBERG that the exephippia females of *D. magna* may produce ephippia. It must, however, be emphasised that we do not know if these ephippia are the result of an impregnation.

Furthermore the ephippia have not been hatched, and it is highly improbable that they have contained ripe eggs. More convincing is an experiment by WOLTERECK (1911 p. 125). If ephippia of *Hyalodaphnia* were kept dry for four months longer than usual and only then given the opportunity of development, females occurred which in one of the first broods, and partly actually in the first, produced males; having produced some male broods, the exephippia females themselves produced ephippia. As the ephippia of the far North are commonly laid dry, or frozen in the ice several months longer than in our latitudes and, according to OLUFSEN, are there formed already in the first generation, WOLTERECK's experiment is of the greatest interest showing as it does that exephippia females, deriving from ephippia from the temperate zone but held under arctic conditions, behave as exephippia females of the far North; the main difference is that the production of male broods according to OLUFSEN seems not to occur in the far North.

The rising temperature of the water in connection with the steadily increasing rate of the vertical sinking from the Ice-Age and to the present time, and horizontally from the pole to the equator, have been the main causes of all the seasonal and local variations. The different local races fixed by the disappearance of amphimixis and by isolation have arranged themselves through selection, during active and passive migration, into series of forms ("Formenkettten") whose individual links adapt themselves through seasonal variation to the conditions of the locality. The clumsy forms to which all our summer forms regularly return every year even in the temperate zone, when our lakes offer arctic conditions, belong to the melting period of the ice and to the present arctic region. The slender forms in the summer half year belong to later periods and more southern zones.

Regarding the changes in the shape of the plancton organisms as means by which they seem to reduce the rate of sinking, all being mutually connected and parallel with the rising temperature and the increasing viscosity, vertically through time as well as horizontally from north to south, I concluded that for the plancton organisms it is a *conditio sine qua non* to follow the variations in the supporting power of the fresh water which are again dependent upon temperature and concentration. As we now further know that the temperature, though with fluctuations, has risen from the Glacial Age to the present day, I further concluded that the rising temperature subsequent to the improvement in climate after the Glacial Age was the direct external stimulant responsible for the occurrence of these series of forms. For the plancton *Daphnias* this view is only a further development of that advanced by EKMAN for *D. longispina* (1904 p. 131).

In the series of forms the single units show the widest possible variation with regard to the specific validity. On the whole they were regarded as local races,

which under the same life conditions were fixed in their form. On the other hand if these races were subject to other life conditions, many of them would most probably lose their specific characters and assume those of other races. Upon that point, however, the explorations were unable to show anything. Now after new explorations as well in nature as on the basis of WOLTERECK'S hereditary studies we are able to get a little further. We will therefore return to this question in the last part of this work.

In the foregoing pages it has been attempted to give the main points of the interpretation of the fresh water plancton, its composition, its life conditions and its origin; this interpretation was based upon more than 10 years' uninterrupted study. The work had its strong point in the fact that the exploration was carried on simultaneously in nine of our largest lakes, its weak point in the fact that explorations in the laboratory and regular experiments were not combined with the out-door explorations. In the Plancton investigations this has often been emphasized and the three main lines along which future explorations should be carried on have been distinctly pointed out.

1. A thorough study of the position of the Plancton organisms, especially the Cladocera, in the water layers, and the signification of their own active motion (1908 p. 13).

2. A thorough study of the signification of the moults, their number, the position and interdependence between them, the seasonal variation, and the propagation (1908 p. 248).

3. Experiments carried on with the main object of showing either that the single geographically distinct local races are in reality fixed through heredity, or that they only are fluctuations (1908 p. 260).

Those who have followed the history of planctological work during the last twenty years will know that it is really along these three lines that limnologists have especially worked in this area of exploration. With regard to point 3 we have arrived at no more thorough results and with regard to point 1 much has been broken down which the future will be forced to build up again. Only with regard to point 2 has our knowledge been promoted, especially through WOLTERECK'S exploration, by a series of very valuable observations. The numerous explorations have, however, brought forward a long series of smaller observations relating almost to all parts of the Biology and Morphology, and in these very observations some of the most valuable material is found. —

If I must now try to meet my critics, I shall have to do so provisionally upon their own ground and not in my original field; to dispute not the seasonal variations in the total plancton community but only that of the Cladocera, and almost only that of *D. cucullata*.

WAGLER (1912 p. 347), who is one of those who on the basis of the greatest number of observations and a series of valuable explorations has penetrated deepest into the matter, has summed up my explorations relating to the variability of the Genus *Daphnia* in the following points.

1. The seasonal variation of all races takes place in the following way: the maximum of variation lies in the summer months, the minima in late autumn and spring; the curve of variation has only one node; the winter forms resemble the exephippio females.

2. The greatest growth of A takes place in May, only shortly after the appearance of the colony, and during a very short time, only about 14 days.

3. During life the relative height of the crista diminishes. The young animals therefore possess relatively higher crista.

WAGLER states that these observations "beruhen zweifellos auf unanfechtbare Tatsachen. Anders steht es mit der Erklärung dieser Tatsachen."

The main objections to the buoyancy theories are the following.

1. The seasonal variations by no means always keep time with the variation in temperature. In many ponds the maximum of variation is not to be found in the months with the highest temperature and the minima not in those with the lowest.

2. *Daphnia cucullata* is not as the theory demands originally a subarctic cold water form; on the contrary it belongs to the Central European climate; it can stand even high temperatures and is totally absent in the North.

3. In the cold lakes the crista are higher than in warm shallow ponds.

4. If the viscosity of the water should be the driving force of the seasonal variations, why then are the races of waters with high salinity provided with high crista?

5. The variations in temperature cannot have produced the seasonal variations because in one lake *D. longispina* has seasonal variation in another not.

6. The Cladocera are on the whole not "Schweber" but "Schwimmer". They do not move passively but actively.

7. The position in the water layers of the Cladocera is not horizontal but more or less vertical; the seasonal variations are therefore quite unable to augment the cross section resistance. —

ad. 1.

The buoyancy theory has arisen from studies which have only been carried on in lakes. At that time we possessed no knowledge of the seasonal variation in smaller lakes and ponds. The roundheaded pond races of *D. cucullata* which mainly seem to support the objection were at that time unknown. That pond explorations were regarded as desiderata was mentioned (1904 p. 12; 1908 p. 321). With regard to the lake plancton it has often been urged that the highest development of the crista is found after the highest temperature of the water has been passed. The phenomenon was well known to me and in my eyes needed no explanation. Referring to p. 153 the following facts may be added. The mother animals beginning egg production at the highest temperature and living after the highest temperature has been passed, are induced to produce young ones during their whole period of

reproduction with *A* almost of the same length; the small temperature differences they are subject to in nature during the beginning of the fall in temperature in the autumn are not greater than those which they may be exposed to during their vertical migrations day and night. In our lakes it may amount merely to a fall of about 2—4 degrees, from 20—22° C. to about 18° C. The life conditions for the growth-stages are almost the same as at the highest temperature. Of the nourishment we do not know anything with certainty; in some lakes it is better, in others not so good, in some years in the same lake better than in others. To demand at our present stage of knowledge that the seasonal variations should assert themselves in the very same week as the temperature begins to sink is too much, especially if we remember that very often periods of warm days set in during the period of falling temperature, and that the amount of food varies especially according to the light conditions.

Now with regard to the pond plancton it must in the first place be remembered that life conditions in the lakes of the temperate zone differ very much from those in ponds; furthermore that whereas life conditions in the first-named do not differ very much from each other, they differ greatly in the ponds; furthermore that whereas life conditions in a lake may most probably for centuries be felt by the plancton organisms as homogeneous, they may in ponds be of the most different kind even during a quarter of a century. Ponds have been observed which possessed a well marked "pelagic region" and were populated by a typical pond plancton. In the course of twenty years the ponds became covered with thick carpets of *Potamogeton natans*; in some years the plancton was then restricted to the spring months before the vegetation covered the surface. At last there were only some remnants of the "old" pond plancton left, and the pond was only inhabited by the fauna which belongs to the carpets of *P. natans*.

In 1908 when the plancton investigations of the lakes were finished I had only a slight knowledge of the pond plancton. In the following years, especially in the last five, I have studied it rather thoroughly. It seems quite unintelligible how scientists could expect that life conditions in lakes and in small ponds should be able to act on plancton organisms, viz. *D. cucullata*, in the same manner. Only those who have but the slightest knowledge of the pond plancton would be inclined to conclude that the buoyancy theories were wrong because in the warmer ponds they observed shorter cista than in lakes with the often lower temperatures.

Whereas in lakes the new brood appears regularly in spring either from wintering mothers or from ehippia hatched almost simultaneously, the brood in ponds appears almost only from ehippia; these are not hatched simultaneously and by no means always in the spring; the hatching moment depends upon the position of the water mark line, which differs very much from year to year; it may be highest in spring, but in years with but slight downpour during winter and high in summer it may be highest in the autumn; then some ponds are filled with low crested exehippio females arriving at periods when the water is at its highest tem-

perature. If then these exephippio females are found by a beginner, the buoyancy theory is declared wrong.

This phenomenon has been observed here by Hillerød more than once. Whereas in lakes the highest development of the crests almost always appears a little after the highest temperature of the water has been passed, in ponds the contrary is the case. Here the reduction of the crests begins before the highest temperature is reached. The smaller the pond is, the more obvious is the phenomenon. The phenomenon is to be interpreted in accordance with phenomena treated on p. 141—144.

In connection with this objection another one may be mentioned, presumably one of the worst of all, but which curiously enough no one has hitherto advanced. In many of our lakes we find two species of the same genus both pelagic, both occurring simultaneously, the one has a pronounced seasonal variation, the other none or only a very slight one. In Sorø and Tjustrup lakes we find *D. cucullata* with a pronounced seasonal variation, *D. longispina* var. *pellucida* without it. Very often we find *B. coregoni* and *B. longirostris* simultaneously and in the same lake. The first has seasonal variation, the other but a very slight one, and this seems to go against what the buoyancy theory demands. This phenomenon was regarded by me not as a proof of the incorrectness of the theory, but only as a proof of the fact that here was something which was not sufficiently elucidated. As mentioned on p. 153, it must be admitted that the plancton organisms as well as all other living organisms are not obliged always to react to the claims of the outer medium in the same manner. The claims with regard to the means to diminish the falling motion may be answered (1.) by augmented cross section resistance, by (2.) augmentation of the power of locomotion, by (3.) variation in the metabolism (augmentation of fat production) or (4.) by wandering combined with accommodation to life in deeper water layers as long as the temperature is high. It will always be very difficult to prove Nos. 2 and 3. Theoretically it may be supposed that it will result in a reduction of size and buoyancy organs, in other words that with rising temperatures we shall get reduction series such as really are observed in the *Anuraea*, in *Notholca longispina* and most probably also in *B. longirostris*. With regard to *N. longispina* see especially AMMAN (1914 p. 137) who shares just the same view which has been advanced here. He regards the so-called degeneration in summer as a "rein physiologische Folge der ungünstigen Schwebebedingungen" (p. 145). From the maximum in April to the minimum in August the animal has been reduced in size by 320 μ ; then in September the size increases again.

Without overrating the observation it may be pointed out that it was shown already in 1908 (p. 241) that of our two *Bosmina* species, *B. longirostris* and *B. coregoni*, the first species reacts to the claims with regard to higher buoyancy power at high summer temperatures by sinking downwards through the water layers, living in the summer half of the year mainly below the thermocline; *B. coregoni*

reacts by seasonal variations, and is therefore able the whole summer to live mainly above the thermocline. Later explorations seem only to have confirmed this.

Quite the same result is arrived at by FREIDENFELT (1913 p. 237) with regard to *D. longiremis* and *D. cristata*. *D. longiremis* is a cold water form hardly ever exposed to a temperature above 10° C., always living in the deeper water layers; the species has but a very slight seasonal variation; *D. cristata* is present the whole summer in the surface layers where the temperature is about 18° C.; it shows a very conspicuous seasonal variation, the most aberrant form being var. *Cederströmii* Schodler.

ad. 2.

The critics are quite right in saying that *D. cucullata* is not a subarctic cold water form. But they are quite wrong when they maintain that the buoyancy theory demands this. On the contrary if *D. cucullata* were a subarctic cold water form, then the buoyancy theories would be wrong. They have further totally forgotten that in the Plancton Investigations it was clearly shown that *D. cucullata* is not a subarctic cold water form but belongs to the temperate zone and the Baltic lakes.

The series of forms begins under arctic conditions with low-crested large clumsy forms; it ends in localities not yet determined, but it is certain that the farther one goes south from the pole towards the Central-European highlands, the more slender do the forms become, and a continual increase in the length of the crista is especially observable. Quite similar phenomena may be seen in *B. coregoni*, and the same seems to be the case with the local variations of *Rotifera* and *Ceratium*. The more the local variations in the plancton organisms become known, the more can the particular variations be ranged in series of forms, the starting points of which are in the north. The further one gets away from the pole, the more complicated and ramified is the course of the series; the nearer one comes to the pole, the more simplified is the course, the ramification ceases, and all the branches meet in a few thick trunks. What is especially required for the study of these chains of forms is a detailed account of the local variation in the countries somewhat north of the great Swedish lakes, or in corresponding latitudes and under similar conditions.

Just as on the southern faces of mountains we find localities able to harbour plants which really do not belong to these latitudes, we often find wind-protected localities which harbour plantonts which should not really be expected until further south. Of course irregularities in the chains of forms occur, but these exceptions only confirm the rule. Similar chains of forms were mentioned in this connection (*Lepus variabilis*: white 12 months of the year in Greenland, 8—9 in Norway, 6—7 in the Alps, not at all in South Sweden and Scotland; the form series of snails from Celebes described by SARASSIN, the form series of *Euphrasia* and *Gentiana* described by WETTSTEIN and those of *Alectorolophus* described by STERN-ECK). We will return to this point later on. —

Now somewhere in the chain of forms *D. cucullata* appeared. Nowadays

it begins near the great Swedish lakes. Scientists who have studied arctic conditions often maintain that there we do not find the great variation between life in the littoral region and in the pelagic region of the larger lakes, and also not so great a difference between life in ponds and in lakes as in more southerly latitudes. — Regarding the fresh water plancton as mainly deriving from pond and littoral forms, the plancton organisms may often be arranged in developmental lines beginning with clumsy littoral forms and ending in the narrow elegant plancton forms characterised by the stamp which life in the pelagic region without a supporting plane sets on its organisms. In 1908 (p. 323) I wrote: "The plancton Cladocera can no doubt be considered from quite the same point of view. From the clumsy, strongly coloured pond and pool forms of the genus *Daphnia* with vigorous, clinging and crawling apparatus, teeth on the terminal claws of the post-abdomen, we have the races with slender hyaline toothless claws of *D. hyalina* and *Hyalodaphnia* (= *D. cucullata*)." We can now hold one of two views: Either that *D. cucullata* after the melting of the ice, most probably during the oak period, as the great variation in life in ponds and in lakes asserted itself, was developed from *longispina* races, accustomed itself to life in larger lakes and fixed the racial stamps through acyclye. Or we may suppose that *D. cucullata* which belonged to the old inhabitants of our globe, after the ice disappeared again, took possession of its old domains and during its wanderings towards the north reached as high up as its constitution allows. But whether we follow the one or the other of these two theories, it is rather difficult to understand how the critics can say that the non-occurrence of *D. cucullata* in the arctic is a proof of the incorrectness of the buoyancy theory. It may be permitted to ask if it would fit in better with the buoyancy theories, if the cold arctic lakes were filled with Daphnids with crests $> V$ as is the rule for *D. cucullata*, than with Daphnids the crests of which are only $\frac{1}{3} V$ or not so much (*D. longispina*, *D. pulex*).¹

ad. 3.

The objection that in the colder lakes the crista is higher than in the much warmer ponds may be answered in accordance with and in the same way as 2. If really the plancton organisms developed their buoyancy organs more in ponds with depths of only $\frac{1}{2}$ to 1 m. than in the larger lakes with depths as in my country to 40 m., and in more southern countries to a multiple of 40, this would be a grave objection to the theory. The theory was based entirely upon studies in lakes. Why should it not be correct for these, even if it were shown later on that it was not in accordance with results gained in ponds? If it is correct that all the variations of the plancton Daphnids are strongly promoted by acycly, how then is it possible for

¹ As mentioned above in the Plancton Investigations (1908 p. 314) the plancton community must be regarded as one of the oldest communities of the earth. I therefore entirely disagree with WOLTERECK when he writes (1920 p. 30) without arguments of any kind: "Doch spricht die Wahrscheinlichkeit dafür, dass die Cladoceren-Arten nicht älter sind als die Eiszeitperioden, in welchen die für ihr Dasein notwendigen Seen entstanden sind." —

scientists who have entered into the spirit of planctology to expect that the plancton daphnids which, in ponds, are regularly dicyclic or monocyclic, and according to some authors polycyclic, should be able to assert themselves owing to the demands made by life as pelagic organisms? Furthermore are the demands in this direction for the same species the same in lakes and in ponds? According to my opinion absolutely not. If it is correct that the zone below the thermocline is to be regarded as uninhabitable in great parts by the living plancton, and all the buoyancy organs regarded as means by which organisms are to be held above this line or in special strata of nourishment, why should the organisms be obliged to develop the highest cristae etc. precisely here in ponds which have no thermocline? Furthermore if, as some authors suppose, the motion of the organisms themselves plays a special role for the place of the plancton organisms in the water layers, why should they be obliged to develop the buoyancy organs in localities where they are able to pass through the whole water layer from bottom to surface in the course of less than an hour?

Of course the buoyancy required in a large and in a small water mass at the same temperature and at the same concentration is the same, but between life in lakes and ponds there is the great difference that in ponds the racial stamp as a plancton organism is obliterated by amphimixis, in lakes it is very often preserved by acycly. Furthermore, whereas the buoyancy apparatus have selective value in lakes, they have none in ponds. We may regard a plancton in a pond from one of two points of view (1.) as originating directly from littoral organisms in the same pond; if so, even if they are exposed to higher temperatures than their relations in the pelagic regions of the lake, these temperatures cannot here produce the same development of the buoyancy organs as in lakes. (2.) Or we may regard a plancton in a pond as passively brought into the pond and originating from a lake race, perhaps in the way that a bay or series of bays are cut off from a larger lake or that during its sedimentation this was changed into a series of ponds. Sooner or later in the life history of these originally lake forms, a moment will come when they cannot keep the locality without the formation of ephippia. As soon as these enter into the cycle as a regular occurrence, the ephippio females which are always typical roundheads, and which are never themselves in a particular manner influenced by the buoyancy demands, play a much greater role in the ponds than in the lakes.—The temperature amplitudes to which the acyclic Plancton-daphnids from larger lakes have to accustom themselves under pond conditions are by no means so large in ponds as in lakes; in lakes where they hibernate as freeswimming organisms they pass from 0 to about 20° in our latitudes; in ponds where they only hibernate as ephippia and where these are not hatched until at temperature of 12—14° C., only from 12—14° to about 24°; this last temperature is only reached with us in very few hours of the year, and by no means every year. Whether we regard the plancton in ponds as originating directly from the littoral zone of the very same pond, or passively brought into the pond and now

forced to accustom itself to pond conditions, the result must be the same. In spite of the higher temperature in the first case the buoyancy apparatus cannot be developed, in the second they will be lost. Again it is tempting to ask how is it possible that planctologists with scientific training can regard the reduction of the crista in *Daphnids* and the humps of the *Bosmina* in pond races as proofs against the buoyancy theory. Just this theory must demand that the buoyancy organs should be reduced by pondlife. If the pond studies, after the Plancton investigations were finished, had shown a higher development of the buoyancy organ in ponds owing to higher temperature, then the theory would be in danger, but only then.

ad. 4.

To the objection that the races from waters with high salinity have high crista the following may be remarked. As far as known, we only know such races from the Elbe, Ostsee and Plattensee. I have no knowledge of these races, but neither have others. It may be taken for granted that *D. cucullata* in Ostsee and the Elbe has originated or originates from colonies which have been carried by rivers into the brackish water. How is it possible that scientists with a limnological training can use this as a proof against the buoyancy theory?

Of *D. cucullata* in Plattensee we do not know more than that it has a well developed crista; (DADAY 1885 p. 179; 1897 Teil I, Sek. 9); at all events as far as known, no more is published. It must be remembered that if these colonies originally come from lakes with normal conditions, and this is in all cases most probable, why then should these colonies when carried out into waters with a higher salinity "draw in" their buoyancy organs? It is difficult to see how they should be of any damage to the organism. As long as we do not know how long these colonies have lived under these conditions, (perhaps they may be recruited every year from other lakes), and as long as we do not know in what manner the variations in salinity act upon the moults, etc., it is rather premature to suppose that the presence of high crested *D. cucullata* races in the Elbe and Ostsee may be used as a proof against the buoyancy theory.

ad. 5.

WAGLER (1923 p. 45) writes: "In den Seen der norddeutschen Ebene und der Alpen treten zwei verschiedenen Typen der *D. longispina* auf, der eine ist cyclomorph und durch hohe Helme in den Sommermonaten ausgezeichnet, der andere ist stets rundköpfig und weniger variabel. Wenn wirklich die Temperaturvariation durch die Temperatur hervorgerufen wird, warum ist dann dieser Faktor nur in dem einen See und nicht auch in allen anderen des Gebietes wirksam gewesen?"

To this must in the first place be remarked that in the Baltic lakes we do not find two different types of *D. longispina* but many: one without and another with cyclomorphosis, but this last-named type is again divided into very many types e.g. forms *D. galeata*, *ambigua*, *lacustris*. Furthermore the two main types as well as those belonging to the last-named type with cyclomorphosis are connected with each other.

Naturalists are indeed not easily satisfied. They complain loudly that they never find the missing links in their presumed lines of development. On the other hand if now and then they find such, they are still not satisfied. This is especially due to the fact that they do not interpret the phenomena in the right way. According to its life and cyclomorphosis *D. longispina* is just that transitional stage in the developmental line of *D. magna-cucullata* which the buoyancy theory required. In one pond it is polycyclic, in another dicyclic or monocyclic. In the lake it is often acyclic, in the same locality in the different years, one year polycyclic, the next monocyclic. In one watermass it hibernates as a free-living organism, in the other only as ehippia, in one locality it has a cyclomorphosis, in another none. In one locality we possess a population whose racial stamp perhaps owing to acycly permits a reaction to the regular annual variations in outer conditions by a slight cyclomorphosis; in others populations occur which are more fixed in form, where amphimixis occurs and which the same outer conditions are unable to influence. *D. longispina* is just the species which the main theory of this work required, a species which in one locality possesses a cyclomorphosis, in the other none. —

With regard to the two last objections the case is different; it is quite intelligible that these two objections to the buoyancy theory may be regarded as grave. They have also been regarded as such. A young zealous Swedish naturalist writes that these objections “die speculativen Schwebetheorie auf diesem Gebiete einen ersten aber auf einmal katastrophalen Grundschuss gegeben hat.” The following pages will show if this so-called death-blow is really of so a fatal nature as this true pupil of the Leipzig school, plus royal que le roi il même, seems to suppose.

ad. 6.

The first of these objections is as follows.

The Cladocera on the whole are not “Schweber” but “Schwimmer”. They do not move passively but actively. WOLTERECK has divided the Plancton cladocera into two groups: the “Schweber” (*Leptodora*, *Diaphanosoma*, *Moina*) and the Schwimmer (all the rest of the Cladocera, *Daphnia*, *Bosmina* a. o.). The grave objection that I have had no understanding of this capital fact has during the last few years often been urged against me. Owing to this fact it may be permitted to reprint what I wrote upon that point (1908 p. 11 and 12). “I have never yet succeeded in seeing *Bythotrephes Cyclops* and *Bosmina* take up floating positions. . . . *Bythotrephes* hops about in the aquaria with innumerable small and short jumping movements; it gives one the impression of being an excellent swimmer but not a floating organism. I have never seen it use its long posterior legs as outriggers; it drags the long spine behind it during swimming, and we might think at a cursory glance that this was rather a hindrance. The direction of movement is as a rule distinctly horizontal. If now we remove the spine, which can easily be done with a good pair of scissors, we change the *Bythotrephes* into a dancing figure, waltzing round and round in spirals or closed circles; it finally ends at the bottom from which it never rises

again. The spine has thus actually been a balancing organ which has played the role of moving the centre of gravity, so that a horizontal movement could be possible; further it is a buoyancy organ which in consequence of its point of insertion and the position it gives the body in the water augments the cross-section resistance."

With regard to the "Schweber" I (1908, p. 11) wrote as follows. "In the next year I received SCOURFIELD'S well known paper relating to the swimming peculiarities of *Daphnia* and its allies. In the years 1902—1908 I had almost always living plancton organisms in my laboratory; their swimming modus and their positions were very often observed. Experience showed me that it is exceedingly difficult to conclude anything from studies in aquaria as to the normal position of plancton organisms and especially to understand the importance of their buoyancy organs. As soon as living planctons are placed in aquaria they come into water to the specific gravity and viscosity of which they are not for the moment suited, it is only rarely we are able to give them sufficient quantities of water from their natural home, and even if so, it will soon be altered on standing. The rate of sinking is either greater or less than that to which they were previously accustomed, and however one may try, the light is almost always, at least during the observation, from one side. As a result the plancton is almost always in motion, and we generally get the impression that the active movements of the plancton are very great; floating stages have only seldom been seen. I have noticed this best in *Atax crassipes* and in *Diaptomus*; I have also seen this several times in *Leptodora*. As far as I understand, the lengthening of the swimmerets by no means augments the swimming power, the long swimmerets being mainly used as outriggers". The objection that the swimming movement of the Plancton cladocera has been underrated, and that the difference between "Schweber" and "Schwimmer" has not been pointed out, cannot be said to be correct.

Having now read WOLTERECK'S paper, I have observed the movements of the so-called "Schweber" organs. In the freshwater plancton we only possess one single real floating organism, the larva of *Corethra plumicornis*, which has transformed its tracheal system into a wonderful floating apparatus; the substance which is used is distilled water or air. In freshwater we do not possess any zooplancton which is able to float only by means of augmentation of the cross section resistance. Perhaps it might be the case with some of the Plancton rhizopods, especially *Staurophrya elegans*, but owing to want of material this rather rare organism could not be examined. Of the other organisms *Atax crassipes* may be said to come nearest to the ideal. But far behind them come the so-called "Schweber" between the Cladocera. Of these I have never seen *Moina* take up "Schwebestellungen". The clumsy big form living in ponds rarely with a depth of more than $\frac{1}{2}$ M., and often swimming directly over the muddy bottom, sinks slowly downward when brought into an aquarium with a water column of half a meter. Of all the Cladocera, *Diaphanosoma* is unquestionably the organism which has the greatest floating power. Of this I had no understanding in 1908. It is quite right

that *Diaphanosoma* is able to hang in the water layers in almost every position. But apart from the fact that its body seems to be as light as the volume of water which it displodes, this is also due to the peculiarly formed second pair of antennæ which are used as outriggers. Now we should have expected that *Leptodora* at all events in just the same degree as *Diaphanosoma* would be able to take up floating positions. This, however, seems not to be the case, at all events in aquaria. Only

very rarely have I seen this with regard to *Leptodora*; they almost always swim, and that in the very peculiar manner that for every stroke forward the animals go a little back. It is as if the swimming motion were taking place in a fluid of high viscosity.— Apart from the significance of these organs as outriggers, it must be strongly

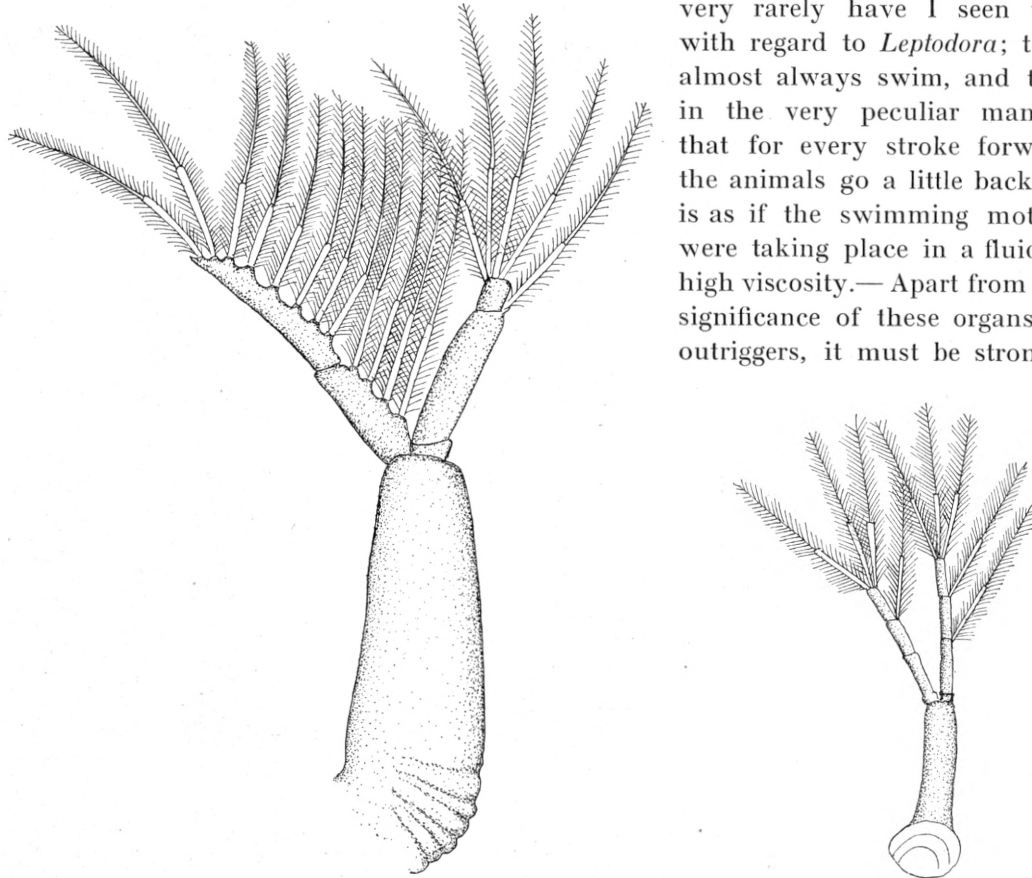


Fig. 10.

Second pair of antennæ of *Diaphanosoma* and of a *Daphnia*. Size of both animals about 2 mm.; drawn with the same power. About 120 \times .

emphasised that in contrast to the first pairs of antennæ in *Diaptomus* they are also, and especially by *Leptodora*, in a much higher degree used as powerful locomotoric organs, fitted for that function by the fasciation of all segments, by their numerous and very strongly feathered hairs, and their very strong muscle system. Only a glance at the two figures (fig. 10) drawn with the same power will show how very much better than in *Daphnia* the oars in *Diaphanosoma* are

suited as well for locomotoric organs as for outriggers. The enormous action radius, especially in *Leptodora*, the very long and very slow strokes, are able to drive them through the water; the insertion far away from the centre of the body is able to keep them horizontal.

Especially with regard to *Leptodora* it is a question if these organisms may really be regarded as "Schweber". Also these organisms are mainly "Schwimmer", but only in a different manner from *Daphnia* and *Bosmina* as these organisms

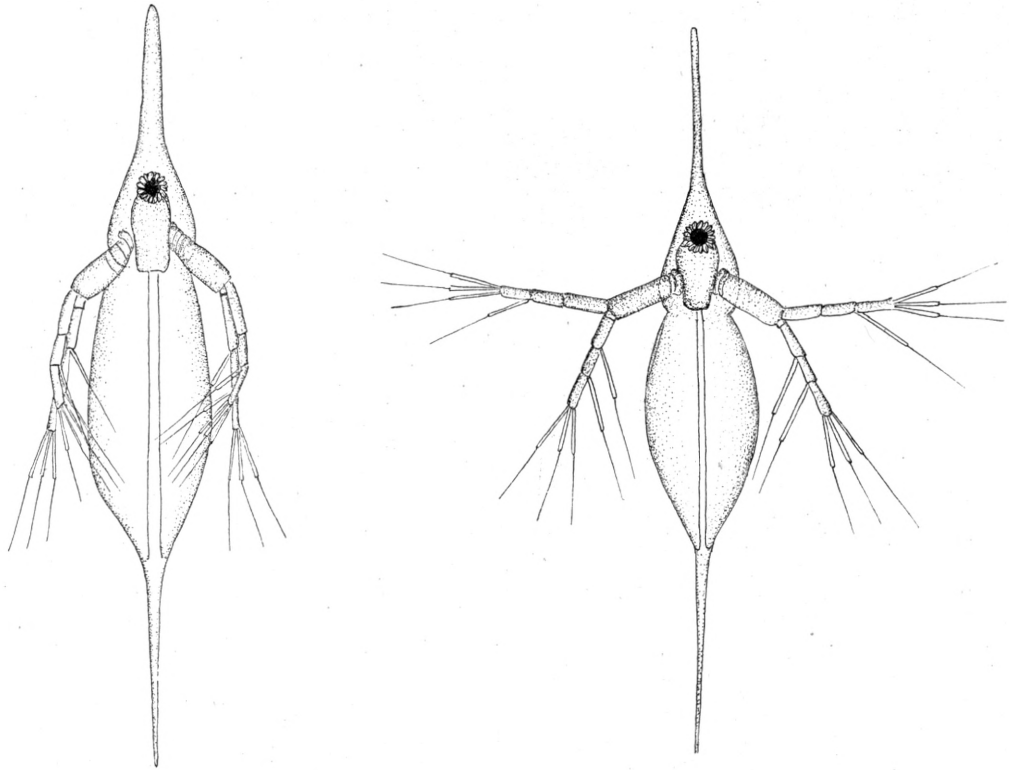


Fig. 11. *D. cucullata* from below, compare with Fig. 12. 30X.

swim with many rapid strokes and with the body held in a slanting position, while the former swim with very few very strong strokes and the body mainly held horizontally. With regard to the length of the way covered between two strokes they may be said to be the best swimmers of all *Cladocera*. The great floating power of *Diaphanosoma* may partly be due to the same ability.

According to WOLTERECK just these organisms lack all those organs which should be used as means to augment the cross section resistance; this is supposed to be in accordance with the fact that these organisms (*Leptodora*, *Diaphanosoma* and even *Moina*) have so nearly the same specific gravity as the surrounding

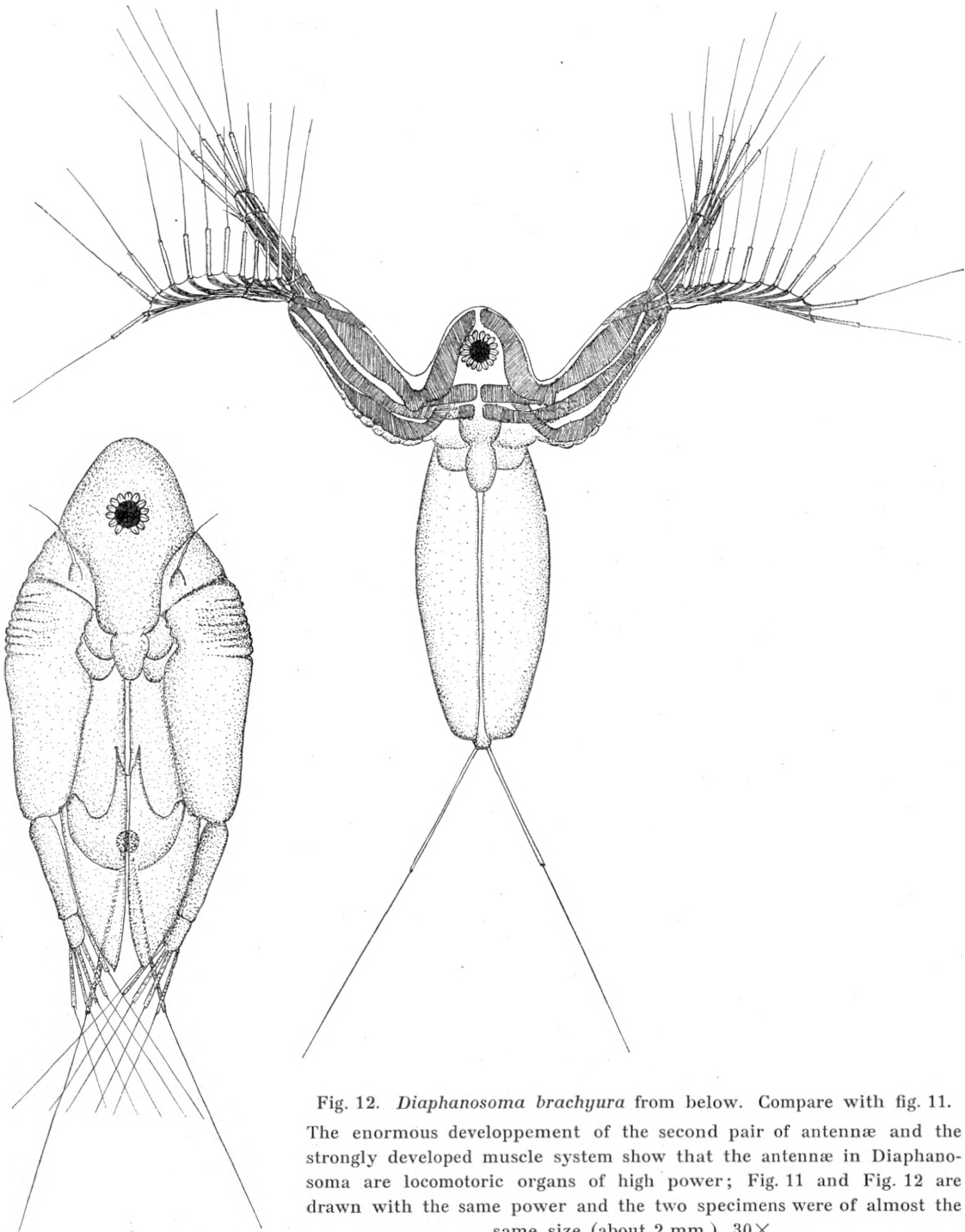


Fig. 12. *Diaphanosoma brachyura* from below. Compare with fig. 11. The enormous development of the second pair of antennæ and the strongly developed muscle system show that the antennæ in *Diaphanosoma* are locomotoric organs of high power; Fig. 11 and Fig. 12 are drawn with the same power and the two specimens were of almost the same size (about 2 mm.). 30X.

medium "dass die Tiere nach jedem Schlage in scheinbar beliebiger Lage im Wasser stehen bleiben. Der Körper hat überhaupt keinerlei Schwebapparat nötig da sein spezifisches Gewicht dem des Wassers gleicht".

This sentence, as is often the case with WOLTERECK's publications, is nothing but a postulate, and even if it contains part of the truth, this has been given too massive an expression.

Quite as unintelligible is WOLTERECK's argument (1913 p. 7) that the fact that the "floating apparatus" ("Fortsätze oder Verlängerungen des Körpers") are absent in the "Schweber" and only present in the "Schwimmer" "allein geeignet ist, uns etwas misstrauisch gegen die überwiegende Bedeutung oder aber gegen die bisherigen Deutung der Schwebefortsätze zu machen." Strangely enough THIENEMANN (1914 p. 658) seems to share the same view. He says that just this fact "allein müsste uns gegen die bisherige Deutung dieser Organe als Schweborgane stutzig machen". To me it seems in confesso that organisms able to float owing to their specific gravity alone of course do not develop floating apparatus, and further, that these should necessarily reach their highest development just in those organisms whose specific gravity is not and cannot be brought in accordance with that of the surrounding medium.

If the buoyancy theory is correct, it must demand that apparatus destined to augment the cross section resistance should be found just in the "Schwimmer" and of course not especially in the "Schweber". And this is actually the case.

ad. 7.

The gravest of all the objections to the buoyancy theory seems to be that the crista, during swimming, is not carried horizontally as the theory requires, but vertically; it should therefore "gar nicht" be able to contribute to the cross section resistance. With regard to this point I have (1908 p. 11) written as follows: "It was with no little astonishment that I observed in 1902 that the long crested summer *D. cucullata* never took up any horizontal position, but remained very oblique, sometimes even almost vertical. The same observation was made as regards the sack shaped *Asplanchna*". At p. 12 I wrote: "Amongst the few *Hyalodaphnia* remaining in the centre of the aquarium I believe I have noticed the following. The normal floating position is, I believe, an oblique position of about 45° with back upwards. Between each movement of the swimmerets *D. cucullata* like *Diaptomus* sinks down in the water; each beat of the swimmerets raises the animal up, and one notices at the same time that the animal with each beat comes to lie more horizontally; before the next beat the animal is again in an oblique or often vertical position with the posterior part sinking downwards. It is furthermore noticed that *D. pulex* is more active with a constant hopping movement, but that we also here are able to see that the forepart of the body likewise with each stroke comes to bend forward. These observations relating to *D. cucullata* are quite opposed to the requirements demanded by the buoyancy theory; the theory must therefore be somewhat

modified. I still believe that the long crest of *D. cucullata* is a buoyancy apparatus, which increases the cross-section resistance of the body and diminishes the rate of sinking. This is attained however, not as we have hitherto believed simply by an increase in the longitudinal axis, as this is not the horizontal axis of the body, as hitherto thought, but the vertical. The formation of the crest increases the cross-section resistance by the shifting of the centre of gravity of the body, so that the original vertical axis actually becomes the horizontal axis with each beat of the swimmerets."

With regard to *Bosmina* I wrote (1908 p. 228): "In *Daphnia* and *Hyalodaphnia* we are able to show that the seasonal variations lead to proportions of the body which are really able to diminish the rate of sinking, but this is not so evident in the *Bosminæ*. The seasonal variation causes the body to increase not in length but in height. On observing the *Bosminæ* when swimming, I found that the position taken up by them is not the same as that in which they are figured. The back very often slopes downwards; if this is the regular position in swimming, H is virtually the longitudinal axis, and seasonal variation would serve the same purpose here as in the other Cladocera; but it is doubtful whether what I have observed is normal. The first pair of antennæ are in any case never used during movements; they hang down like long immobile rods. One might feel inclined to look upon them as floating apparatus, but if H is the vertical axis they are placed parallel with the direction of sinking and not at right angles to it, as is almost always the case with floating apparatus intended to function as a balancing organs".

P. 13 I added: "We must add, however, that more exact investigations are still desired concerning the normal position of plancton organisms in the water, in order that we may learn with certainty that the buoyancy organs are really placed horizontally to the direction of sinking. It should further be mentioned that the increase of the longitudinal axis at least in many cases will only increase the cross-section resistance, if the normal vertical axis of the animal becomes the horizontal; this becomes possible as so many of the so-called buoyancy-organs are likewise of importance in shifting the centre of gravity, without which horizontal movements would not be possible." It will be understood that the phenomenon that the vertical axis of *D. cucullata* is carried vertically was by no means unknown to me; I only had another apprehension of it. The observations having shown that the different seasonal variations in very many planctons begin simultaneously, reach their highest development at the highest temperature, and again diminish at lower ones, and furthermore that the pronounced summer forms with their peculiar shape (*Holopedium*, *Leptodora* a. o.) just arrive at a moment when the cyclomorphosis begin in the perennial ones, it could be regarded as a matter of fact that the summer plancton had a much higher cross section resistance to counteract a greater falling velocity than the winter plancton. When therefore it was observed that the longitudinal axes of the planctons were vertical and not horizontal, this was to me not a proof of the incorrectness of the theory, but merely evidence that here was something which required a more thorough investigation. It was this which, with

an indication of the way which future explorers should use, was left to my successor. This successor was WOLTERECK, but he set about his explorations in quite another way than I had followed, and his starting point was another. Studying hereditary problems and sexual problems upon Cladocera, he saw that in his vessels *D. cucullata* was standing vertically; further by means of better nourishment he was able to prolong the crest even if the temperature was very low. From these explorations he arrived at two results, in my eyes both wrong: I. The prolongation of the main axis of the body cannot be regarded as a means by which the cross section resistance is augmented. II. The prolongation is in the first place due to better nourishment.

The above-named main point in the Plancton Investigations, that the cyclo-morphosis of the few perennial Plancton Cladocera coincides with variations in the whole Plancton community has either never been understood by WOLTERECK, or he could place no confidence in it.

As his main results were, however, opposed to a theory which had some standing, a whole lot of young people were set to gather material against it, and to support his theory that the development of buoyancy organs was due to better nourishment. Some of his pupils began regular explorations, but all only in a single water, and always only with regard to one or a few species, never with regard to the entire freshwater plancton; most of the explorations were, as mentioned above, carried on in ponds. WOLTERECK who has never himself worked with limnological problems, is responsible for the fact that his young scientific co-workers never understood that the conditions for buoyancy do not assert themselves in the same way in ponds and in lakes, nor that the buoyancy theory is not wrong, nor should be altered because the organisms under the very varying life conditions in ponds and lakes are not able to react to the buoyancy requirements in the same way. Of course one of the first explorations gave the desired result that the theory was incorrect; a long series of papers, almost all based upon studies of a single or a few species, and mainly pond species, now appeared; all took decided ground against the buoyancy theory, and all arrived at the same result. This has further caused that NAUMANN has, in a series of papers in many of which is almost printed quite the same thing, from single casual observations and with a very fugitive literary knowledge, spent a deplorably great part of his youth in proving that the buoyancy theory is superfluous in every direction and its foundation wrong. We will now discuss WOLTERECK's two main results.

I. The prolongation of the main axis of the body cannot be regarded as a means by which the cross section resistance is augmented. If we take the three well known figures of WOLTERECK, unquestionably quite correct, to show the shifting of the main axis of the body during the movement, it is evident that in figure II the spine and the crista will act entirely in accordance with the buoyancy theory. This position represents the pause between two strokes of the antennæ, just that moment during which the buoyancy-organs as means by which the cross-section resistance

is augmented are to assert themselves and in virtue of their existence hold the body upright till a fresh stroke with the antennæ again prevents the fall. WOLTERECK seems to have no understanding of that which is the chief point of all: that if the buoyancy organs should really help the organism, it must be in the pause between the two strokes of the antennæ: during the strokes the animal "could help itself". WOLTERECK has underrated the pause and its significance for the falling velocity. OLUFSEN, too, has quite the same result in his excellent work upon the Crustacea of Spitsbergen (1918 p. 415).

WOLTERECK'S views are in accordance with his supposition that the development of the buoyancy organs is in the first place dependent upon variations in nourishment. Even if WOLTERECK is able by means of better nourishment at low temperatures to develop the crests of the *Daphnia* and by insufficient nourishment but at high temperatures to diminish their size, these interesting results are of no importance whatever with regard to the significance of the buoyancy theory as a working theory for future explorations, owing to the fact that the compact plancton community in summer possesses a smaller falling velocity than in winter. They only show what has always been urged that better nourishment is the means by which variations in the outer medium are able to assert themselves, but from this to regarding variations in nourishment and temperature without due consideration for variations in viscosity and specific gravity as a main factor there is a very long step.

It is WOLTERECK'S great merit to have tried to show in what particular manner the buoyancy organs act. Especially in the case of the *Bosmina* body he has given a very fascinating picture of the significance of all those peculiar structures which before him no one has hitherto had any understanding of. I refer especially to his work of 1913 p. 502—512. Also his explorations with regard to the number of moults (1920 p. 74) and the postembryonic development have revealed a number of new and valuable facts. His designations *Neonatae*, *Primiparæ* and *Terminales* for the stages of the first moult, the female which carries the first set of eggs, and the female which has completed its growth, are very valuable. In the Plancton Investigations I have tried to distinguish the same three growth classes, the full grown animals, the growth stages, and the newly hatched brood; in the tables by means of two lines these three groups have been kept distinct. As all the explorations were carried on in Nature this could not be done with the exactness at which WOLTERECK has arrived.

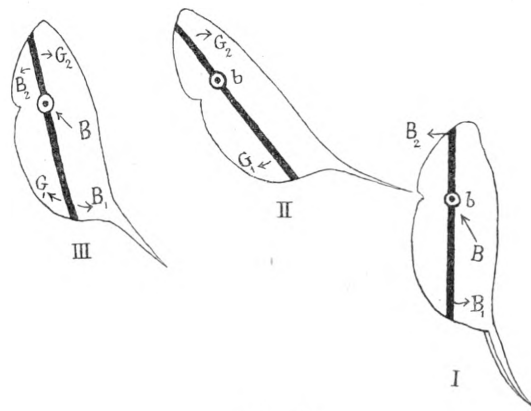


Fig. 13.

The variation in the position of the axis during the swimming motion of a *Daphnia*. Fig. II represents the pause between two strokes of the swimmerets. After Woltereck.

The weak point in his explorations is that observation and speculation have not been kept distinct, so that we cannot see where the former stops and the latter begins. Just as regards those main points where it is of the greatest significance, it is quite impossible to see what is observation, and what may merely be designated as a clever davenport theory. Especially with regard to the *Bosmina* races the great question is: Has WOLTERECK really seen the *gibbera*, *tersites* forms swim in the position which he has figured in fig. 2 e. Are his pictures based upon deductions or observations? These summer forms are rare, and they are extremely difficult to observe. During the summer of 1925 I visited Juullake in Jutland where the *gibbera* races are most conspicuous. The living organisms were kept for several days in jars in my room. The *gibbera* forms swam in very many directions, by no means always in horizontal lines; very often vertically with their backs turned almost downwards, by no means with that regularity which WOLTERECK's theory seems to demand. What we still lack are thorough explorations relating to the position and behaviour of the living *Bosmina* races. WOLTERECK's entire chapter on the structure of the *Bosmina* races certainly looks extremely enticing; it may be correct, but the real proof of its correctness viz. observations of the motions of the living animal, has in my opinion not been given.

How fearlessly W. draws conclusions from observations in the aquaria as to the real life conditions in Nature will best be understood from the following fact. Because WOLTERECK has seen that the *Daphnia*, when kept in a cup glass, on pushing off from the bottom with the spine, moves upward, he writes: "das Aufstossen der Spina auf dem Grund löst sofort lebhaftere Schwimmbewegungen auf welche vom Grund wegführen". From 1920 p. 61 it will be understood that he thinks that the contact with the bottom of the lake by means of the spine is also here of significance because it "eine schnelle Folge der Ruderschläge und dadurch ein Aufsteigen verursacht". How is it possible that a scientist with a limnological training can really suppose because he has seen a *Daphnia* touch the bottom of a cup glass with the tip of the spina and move upwards as a result thereof, that the spine should have a similar significance in Nature?

That the animals, because they moult every second day in the vessels at a temperature of c. 20°, should also do so in Nature, I regard as highly improbable; also that they should reach the same size between two moults in Nature as well as in vessels; further that the animals after a number of moults in Nature should not grow any more may be regarded as highly problematic; here as so often it may be supposed that WOLTERECK has concluded too much from the observations in the vessels as to life in nature.

On the whole, if we wish to designate the spine and crista and all the peculiar structures of the *Bosmina* body as means to a "Horizontalisierung der Schwimmbanen", we may really do so. On the other hand, it must be admitted that this is a rather farfetched phrase which veils the fact that this supposition is not so new as it seems to be. It must well be remembered that organs which serve the

organisms in that way viz. to hold them above the thermocline, may also act as structures which govern the rate of the falling velocity i. e. act as buoyancy organs. Upon that point there can be no doubt at all. Therefore it is also quite intelligible that not all have admitted that WOLTERECK and his school (see especially the many peculiar papers by NAUMANN) are right in their supposition that WOLTERECK's work has rendered the buoyancy theory superfluous. All Woltereck's work upon that point is based just upon the buoyancy theory; without that it would be left suspended in mid-air.

II. As mentioned above, WOLTERECK has arrived at the result that the development of the buoyancy organs is dependent upon better nourishment. According to him the buoyancy organs are means by which the organisms are prevented partly from sinking below the thermocline and partly from being caught by the surface film; in the first place, however, they hold them in those strata of nourishment in which the nannoplankton must live.

It has often been said that with regard to the development of the buoyancy-organs I have underrated the significance of the variations in nourishment. Before entering upon the discussion with regard to the dependence between zooplankton on the one hand and thermocline, surface film, and nannoplankton on the other hand, we will shortly examine the correctness of this first-named objection.

It is a matter of course that in spring, when the temperature rises and we see the huge maxima of Diatoms, Flagellata and Chlorophyceae develop, the food supply of the zooplankton must be augmented. Then the assimilation energy of the Cladocera is also increased. The result hereof is again that the parthenogenetic propagation goes on simultaneously with increasing velocity; further that the number of moults, that is to say the number of intervals during which variations in outer conditions are best able to assert themselves with regard to corresponding variations in the outer shape of the organisms, is augmented (W.-L. 1908 p. 248—249). It was here mentioned that the moults most probably went on at a much slower rate in the winter than in the summer half of the year. "It must be the task of the future through experimental investigations on isolated individuals of the same brood but under different conditions to ascertain the influence of the latter on the organisms during their growth. In collecting and drawing the various skins, in noting the dates of each moult which each individual undergoes under different conditions, the influence of the latter on the moulting, and thereby on the seasonal variations, may be more definitely determined."

Now it is just these explorations which WOLTERECK has carried on. It is WOLTERECK's great merit that he has carried through the long and valuable series of experiments just as to the influence of variation in nourishment upon the variations in outer form of the *Daphnia* races. However, because W. has only worked in the laboratory, and because his studies were mainly on heredity, he has very much exaggerated the scope of his results.

From my own studies I was so to speak forced not to find the main cause for

the development of the buoyancy organs in variations in the amount of nourishment. I have by no means overlooked this factor, but when I have not been able to place it in the first line it is from the following considerations. I cannot see better than a future, viz. NAUMANN'S explorations, upon that point have confirmed my views.

Owing to the fact that it is not a single organism but a community, the single members of which simultaneously undergo seasonal variation and follow each other, we are obliged to suppose that there must be an outer factor which during immense spaces of time has forced, and to this very day forces, the plancton organisms to form variations. As the organisms follow each other in their change of form, and all seem to aim at the same object, this outer factor may act with a quite regularly augmenting and then quite regularly diminishing intensity. As apart from smaller local manifestations the seasonal variations over immense areas in thousands and thousands of localities everywhere keep step with each other, this outer factor must over immense areas act, if not with the same intensity everywhere, still on the same lines, and in the same way.

The question is now: Can we say that the yearly annual variations in nourishment in a single locality and in thousands of localities over immense areas take place with the regularity demanded if variations in nourishment were to be made responsible for the seasonal variations? All planctologists will know that this question must be answered absolutely in the negative.

IN WOLTERECK'S considerations the term nannoplancton plays a very prominent part. We will return to this term later on, and for the present content ourselves with the following brief remarks. The main food of the Cladocera, at all events of the Plancton cladocera, consists of the smallest individuals of the phytoplankton; in some parts of their area of distribution, especially in waters with high acidity, and during some periods of the year of the finest floccous detritus; shortly expressed, at our present stage of knowledge we cannot get nearer to the truth.

It is now a well known fact that over great parts of the temperate zone and in very many lakes the phytoplankton possess two large yearly maxima, one in spring and one in autumn; these maxima are formed by Diatoms and some flagellates especially *Dinobryum* and *Ceratium*; in many lakes in which Cyanophyceae only play a rather insignificant role, we find a conspicuous summer minimum for the phytoplankton; in other lakes where the Cyanophyceae prevail, the greatest maxima for the phytoplankton appear precisely at the highest temperature. The greatest phytoplankton maxima I have seen have occurred in October—November and were due to enormous amounts of different plancton diatoms. The maxima of the phytoplankton during winter vary from year to year in the same locality. In winter when the lakes have been frozen over for 100—140 days, the amount of phytoplankton is extremely small, in winters when the lakes have not been frozen large maxima of *Melosira*, *Asterionella*, *Fragilaria*, *Peridinium* and *Dinobryum* may develop at temperatures between 0—4° C. In lakes which are in the transition stage

between lakes and ponds the Cyanophyceae may in warm summers develop incredible plancton maxima, but in cold ones be little pronounced. If the amount of the phytoplankton is exceedingly variable in lakes, not only seasonally in a series of years in a single lake, but also from lake to lake even over a rather small area, it varies much more in ponds. No one has studied the phytoplankton in a series of ponds regularly every 10 days during a series of years without being struck by the enormous variation in the phytoplankton, not only in the same pond from month to month, but also in the same pond and in the same month but in different years. The variation is most striking if the explorations are carried on at the same time in a series of ponds lying at a distance of only a few yards from each other; see also the excellent studies of LIST (1917 p. 56); my own hitherto unpublished pond explorations will show the same. The same pond may in one month have pure zooplankton, in the next almost pure phytoplankton; in one year *Ceratium hirudinella* may colour the water yellowish in August, then disappear and not appear again till six years later. One pond has an enormous zooplankton, and clear water without phytoplankton, another, lying quite near, simultaneously an enormous *Dinobryum*, *Ceratium* or Chlorophyceae maximum; in both *D. longispina* appear in races which cannot be distinguished from each other. The phytoplankton of the ponds may be distinguished from that of the lakes by the fact that the enormous maxima which we find in ponds are only very rarely observed in lakes. — In areas where we may reckon with detritus as the main food of the zooplankton, this is in the first place dependent upon the position of the lake, the quality of the bottom, the force of the wind and the number of gales during the year. It may commonly be said that it is greatest in autumn and in spring, especially immediately after the ice has broken up and eroded the shores and carried an enormous amount of detritus material out into the water layers.

It will be clearly understood that a factor which is exposed to such enormous temporal and local variations as the amount of food material, cannot be that factor which determines the seasonal variations which all in all run parallel with each other, and are initiated, reach their climax, and diminish simultaneously. A factor which varies constantly both temporally and locally cannot produce a result which must strike all who will and can see by its regularity.

Further, if seasonal variations were dependent upon variations in nourishment, we should in various respects expect (1—5) to find a concordance which is totally lacking.

1. As mentioned above, in very many lakes we find, just at the time when the seasonal variations and especially those of *Daphnia* and *Bosmina* reach their climax, a very pronounced minimum of the phytoplankton; just at that time the temperature is highest and the viscosity lowest.

2. The greatest maxima for the phytoplankton are often reached in spring and in autumn. It would indeed be very peculiar if the greater amount of nourishment should be primus motor for the seasonal variations in spring, whereas the same or often much higher amount in autumn should cause their decrease. Just at the

time when the floating apparatus "are drawn in", the temperature falls and the viscosity increases.

3. If better nourishment should cause the seasonal variation, it would be a very peculiar phenomenon that the roundheaded, very small, so-called "Kümmer-rassen" appear in the ponds where the amount of phytoplankton is commonly much higher throughout the summer than in the lakes, and where the large forms with their highly pronounced seasonal variations appear.

4. All authors are agreed that the maximal size at all events very often and especially in the case of the *Daphnia* appears in spring at a temperature of 8—10° C. Then before the phytoplankton maxima occur, we find the thick clumsy forms with very broad and very large valves, and with the greatest total length. At the highest temperature in summer, the size decreases conspicuously; both in larger lakes where the quantity of phytoplankton is in some lakes enormous, in others small, and also in very many lake ponds where Cladocera during the whole summer so to speak live almost in a regular plankton porridge, we get narrow slender forms; often the valves are neither in height nor in length more than half of that in spring. Simultaneously with the augmentation of the length of the crista, the length of the valves or the length of the spina or in some cases of both diminishes. — In one of the papers from the last few years LIST (1920 p. 791) comes to the same result.

Experiments in the laboratory show the same: in very many cases the size diminishes simultaneously with improvement in nourishment; what is augmented is only the crista. If nourishment had caused the seasonal variations it might have been expected that the size of the whole organism would have been augmented together with the excessive growth of the crista. Even if the size of the organism had remained unaltered, and only the crista had been augmented, this would have been intelligible, but to assert that better nourishment should create long crests in organisms which simultaneously diminish in size, whose V is smaller, and which only reach about $\frac{1}{3}$ volume of the big spring forms, that is too much. In the whole animal kingdom we only find very few examples of the phenomenon that an excessive amount of nourishment produces a very restricted growth of special parts of the body (e. g. the hump of *Camelus*). But in the whole animal kingdom it will probably be still more difficult to find examples which show diminution in size combined with excessive growth of special parts of the body due to better nourishment.

5. Besides it must not be forgotten that better conditions of nourishment can never elucidate the seasonal variations in Diatoms and *Ceratium hirundinella* nor explain why the periodical plankton organisms appearing in the summer half of the year are provided with buoyancy organs, perhaps most conspicuous in the numerous plankton Chlorophyceae all belonging to the summer half of the year.

Among all the numerous explorations carried on in Nature it will be very difficult to find a single one which supports WOLTERECK'S view that they must be understood on the supposition that variation in nourishment, without any re-

gard to the much deeper cause, the regular annual variations in the bearing power of the freshwater, could alone explain the phenomenon. On the other hand, explorations in Nature very often show accordance with the opposite view. We will now in accordance with Woltereck's view discuss the plancton in its relation I. to thermocline, II. to surface film and III. to nannoplancton. At last IV. we will mention the explorations of NAUMANN a. o. relating to the nourishment in the Plancton cladocera in Nature.

I. Plancton in Relation to Thermocline.

As mentioned above, WOLTERECK is of opinion that the home of the Plancton cladocera is to be found in the midmost water layers. Those below the thermocline will perish, and in the surface film they will be caught. As WOLTERECK expresses it, the life of many *Daphnia* races is passed between a Scylla and a Charybdis; both have selective value, all individuals which are not able to follow sufficiently horizontal courses are caught by one of them, and death is then the result. At this really sad conception of the life of the poor Plancton daphnids WOLTERECK has arrived from his studies of Plancton cladocera in very small volumes of water, where the crista really very often touch the surface and the spine the bottom. In the lakes with water columns often of many meters it is to be supposed that the distance between Scylla and Carybdis is so large that a considerable number may die a natural death between both.

In this connection it must not be forgotten, firstly that BIRGE and JUDAY (1911 p. 249); BIRGE (1914 p. 62) and BEHREND (1914 p. 71) have all found large maxima of plancton crustacea below the thermocline, and secondly that all in all we lack regular observations, taken with horizontal closing nets below the thermocline. At our present stage of knowledge we may be entitled to suppose that the water layers below the thermocline are unfitted for most of the Plancton cladocera, and that their real home is mainly above it. But from this result at which all plancton investigators before Woltereck have already arrived there is a great leap to regarding the hypolimnium as the Scylla for all those "in nicht genügend flachen Bahnen schwimmenden Individuen".

WOLTERECK maintains that he possesses observations ("bisherige Untersuchungen" 1913 p. 522) which show that below the thermocline we mainly find older animals with low crests; he seems to share the view that the Daphnids are stratified in accordance with the height of the crista; those with the lowest crista stand nearest the bottom. How these observations were carried on and where, WOLTERECK does not say; and in his work of 1920 we only find repetitions of what he has said in 1913. In the literature I only find one single observation which seems to corroborate the view of WOLTERECK. LIST (1920 p. 791) says: "Von Januar bis April lebt die *Daphnia* als plumper breiter Rundhelm in der Tiefe". The animals arrive at the surface in May, mainly young animals with well developed crista.

In June (Furesø 1912—14) I have shown by means of the Nansen closing

net, used regularly every eight days at 35—30—20—10 m., that the low crested hibernated winter forms were really to be found in the deeper water layers, whereas the surface layers are populated mainly by the higher crested summer forms. The low crested winter forms from deeper water were all barren and represented the dying out forms, which having now finished reproduction in the surface layers, were sinking downwards. These observations seem to corroborate the views of WOLTERECK and LIST, nevertheless I do not think that the explanation of Woltereck is correct. For during the whole winter the roundheads may be caught in the upper layers of our lakes. During the winter of 1924—1925 I have taken them in the surface in the lake of Frederiksborg Castle with $\frac{1}{3}$ of the net above the waterline. The old Daphnids sink downwards when their life is finished, and this has nothing to do with the form of the head. In spring the deep water Daphnids are roundheads and the surface daphnids high crested, because the first-named are the wintered autumn-brood, now dying out, the last named the young animals; in autumn because the low crested old forms during moults have reduced their crista and after egg production now sink downwards, whereas the primiparæ and those which still have to produce some broods, all having well developed crista, are to be found in their real home very near to the surface. —

II. Plancton in Relation to the Surface Film.

Whereas WOLTERECK at any rate speaks with some caution as regards the thermocline, with regard to the surface film he is more confident: "Klarer ist mir die Beziehung zum Wasserspiegel". Just in this very point of WOLTERECK'S deductions and observations I confess I have no confidence. —

The significance of the surface film for the fresh water plancton is all in all badly understood. In our Danish lakes the surface film probably plays a rather prominent role. It differs very much from lake to lake, it is mainly of significance at higher temperatures, mainly on calm days, more in lakes with high Cyanophycé maxima and during the development of these than in lakes without such. Owing to the enormous quantities of dying Cyanophycé material oil globules are always liberated and deposited upon the surface of the lake. If the surface is skimmed, we find numerous Daphnids, the skins of which are covered with hundreds of very small oil globules especially hanging as pearls in the hairs of the antennæ. Most probably it is in this very thin layer of oil covering all our lakes, especially our Cyanophycé lakes, and mainly after their highest maxima, that the Cladocera are caught. Especially in autumn our small lakes rich in organic matter carry on their surface enormous quantities of Daphnids, most of them provided with ehippia. The slightest breeze will carry the whole material to the shore, and there it will form a dark brim of ehippia, dying animals and skins. The small bays on the wind coast are filled with a greyish dust which is later on deposited on the shore as a peculiar glassy brim in which during winter and spring a rich life of the larva of Diptera is developed. Just at that time, when the surface of these

lakes is covered with skins and dying animals, the minimum of *D. cucullata* sets in, the animal almost disappearing from the lake.

The most peculiar fact is that the different planctons in their relation to the surface film show very different degrees of affinity. All the *Bosmina* species and *Brachionus pala* may all be caught by the surface film; *Diaphanosoma*, *Leptodora*, *Bythotrephes* and *Chydorus* which plays a prominent part in the plancton of many Cyanophycé lakes, on the other hand, are never caught by it. Among the Rotifera the same is the case with *Asplancha*. Even if the water may be milky in spring with enormous quantities of *A. priodonta*, they are never deposited on the surface of the lakes. On the other hand, *Anuræa aculeata* and *cochlearis* are caught. The Copepoda are never caught. With regard to their relation to the surface film see SCOURFIELD (1896 p. 1) Furthermore it is very peculiar that the affinity differs between the single species of the same genus; it is very little pronounced for *D. pulex* but very conspicuous in *D. longispina* and especially in *D. cucullata*.

If we have *D. cucullata* and *D. longispina* in a lake simultaneously, it is the high crested *D. cucullata* which is caught much more than the low crested *D. longispina*. — The same difference in relation to the surface film we find with regard to the bottom and littoral species: some are caught, others not. Almost all littoral Cladocera are caught, e. g. *Simocephalus*, almost all *Lynceidæ*, especially *Eurycercus*.

If we take a plancton sample from one of our lakes especially in summer and pour the material into an aquarium, all the material of *D. cucullata* and *longispina*, *Bosmina* and some of the *Brachionus* and *Anuræa* will be caught by the surface film and cover the surface as a glassy coating; the *Leptodora*, the *Asplanchna*, and the *Diaphanosoma* are never caught. Common to all these planctons is the fact that they are all positively heliotropic and all seek the lighted side of the aquarium; arrived at the glass wall all the *Daphnia* and *Bosmina* may easily be seen so to speak suddenly to jump up onto the surface, be caught by it, and then slowly glide away from the wall; the *Leptodora* and *Diaphanosoma* are carried downwards and are never caught. —

On a comparison of the Daphnids especially *D. cucullata* and the *Bosmina* on the one side and *Leptodora* and *Diaphanosoma* upon the other side, it is obvious that the amount of oil globules, especially in Cyanophycé lakes, and in autumn, is much higher in the first-named than in the last-named. Most probably the first-named in such localities and at that time of the year are supercompensated owing to the large amount of oil as store material whereas the last-named are not. This consideration is so much the more allowable as the plancton species of the genus *Daphnia* almost always possess a much higher amount of oil globules as store nutriment than the pond species (*D. magna* and *D. pulex*). —

Looking at an aquarium surface covered with caught Daphnids, we further find many dead specimens, and the oil liberated lying round the animals; these red oil globules run together and form large red oil masses; a very thin membrane is spread over the surface; looking at the caught material, we get the impression that

it is of a peculiar glassy appearance as if the surface of the animals was "unbenetzbar", an appearance which the surface of *Leptodora* and *Daphnella* never possesses. SCOURFIELD (1896 p. 2) also comes to quite the same result.

In this way we get some leading points enabling us to understand the fact that some of the planctons are caught, others not.

In the fact that some of the plancton cladocera are caught by the surface film I am partly inclined to see an aquarium phenomenon. For the oil quantity in these species is so high in our lakes, so extremely rich in organic matter, that they are so very near supercompensation that their muscle force is unable to counteract the speed with which they were brought upwards owing to the stroke against the side of the vessel. Jumping, upwards they are caught by the oily membrane; in their skins we find no structures which are able to prevent the surface membrane from being broken and, once broken, their muscle force is not strong enough to break it. The animals are then caught. Of significance is certainly also the fact, first alluded to by SCOURFIELD (1896 p. 4) that the caught animals which always lie on one side are only able to use one of the antennæ. Further, it was often observed in aquaria that specimens are liberated by moulting; the old skins remain lying on the surface, the animals themselves swim away; this is especially the case with ehippial females.

From these observations I for my part am inclined to suppose that the surface film in reality plays a much greater role in aquaria than in Nature and here greatest in autumn when the ehippia are to be liberated, that it plays no role at all in Alpine lakes, that it is even of very slight importance in the Baltic lakes during winter, whereas at the highest temperature especially in lakes with high Cyanophyceæ-max. it plays a rather conspicuous role and in autumn is able to change the surface of the lake into a regular churchyard for all those species of planctons whose amount of oil globules is so large that they are supercompensated, their skin being of such a structure that the oily membrane of our lakes can be adherent and make the surface of the animal "unbenetzbar".

All in all it will be understood that the relation to the surface film is a rather complicated phenomenon which cannot be studied from a few observations in a single lake and in a single species. —

As far as known, WOLTERECK has carried on all observations with regard to the surface film in my laboratory, and they all belong to the few observations he has made in the lake by Frederiksborg Castle. By skimming the surface of the lake (1913 p. 522) he gets 62 *D. cucullata* in 150 cm. of water of which 40 carried eggs. In the water layer below, the number of young animals without eggs and with high crests were at least ten times as numerous as the ripe animals. From this observation WOLTERECK supposes he is able to draw the following far reaching conclusions relating to

(1.) the motion of *D. cucullata*, (2.) the significance of the crista in the relation to the surface film. (3.) Lastly he supposes he is now able to understand why

the total size as mentioned above in spite of better nourishment diminishes simultaneously with high development of the crista.

(1.) (2.) The significance of the crista in relation to the surface is supposed to be that the swimming tracks are made so horizontal that it is with the antennæ and not with the crista that the surface is reached. Dorsally directed strokes should then carry the animals downwards; if it should happen that the surface is reached with the crista the animals should be caught by it and then die. W. says: "Es scheint ein fein ausgebildeter und entschieden zweckmässiger Reflexmechanismus für die Berührungen zu sein, die ja auch im Leben der Tiere wichtig genug sind".

(3.) With regard to the third point it is necessary to reprint the following lines: "Eine merkwürdige und bisher unverständliche Tatsache hat sich auf diese Weise wahrscheinlich erklärt: wir finden im Plancton dieses Sees im geschichteten Wasser des Sommers zwar eiertragende, aber nur junge, nicht vollständig ausgewachsene *Hyalodaphnien* (vom ersten bis etwa zum siebenten Häutungsstadium), Tiere also, die nur zwei bis höchstens drei Würfe gezeitigt haben. Im durchgemischten Wasser (Herbst bis Frühjahr) dagegen werden die Tiere trotz der ungünstigeren Assimilationsbedingungen viel älter, so dass wir selbst das zehnte bis zwölfte Häutungsstadium relativ häufig antreffen.

In Kulturen zeigte sich nun, dass die Sommertiere ebenso leicht dieses Alter und Mass erreichen, dass sie dabei aber durchweg kurzhelmiger sind wie die jugendlichen und halbausgewachsenen Tiere. Ihre Bewegungen sind aus diesem Grunde nicht unbeträchtlich steiler und führen zumal in jenem nur 3—4 m. tiefen See viel leichter an den surface film. Mit andern Worten: die ausgewachsenen Tiere gewisser *Hyalodaphnia*-Rassen scheinen im Sommer für die pelagische Existenz in einer begrenzten Wasserzone, also besonders in flachen Gewässern, nicht hinreichend angepasst zu sein." In a Note WOLTERECK remarks: "Ich darf nicht unterlassen, darauf hinzuweisen, dass andere Rassen der gleichen Art grade in flachen Teichgewässern dauern, auch im stark erwärmten Wasser niedrigköpfig sind. . . . Diese *Hyalodaphnia*-Formen (which WAGLER has found in Sachsen and which are common in the central parts of Germany) scheinen, soviel wir bis jetzt sehen, in den dänischen Teichen zu fehlen" (1913 p. 523).

All WOLTERECK's speculations relating to the surface film result in the sentence that the contact with the surface, owing to not sufficiently horizontal swimming courses, has selective value because the animals, when caught, perish, in other words that the surface film is one of those factors which are responsible for the seasonal variation of the crests in the plancton Daphnids.

To this part in WOLTERECK's work I regret that I am forced to say that all remarks relating to temperature, stratification, nourishment and occurrence of races are incorrect. That the same is the case with the deductions cannot astonish one.

As always in WOLTERECK's work observation and speculation are woven into each other, and it is impossible to see where observation ceases and speculation begins. As far as I have been able to follow the deduction of WOLTERECK, it seems

to be his opinion that the Cladocera are caught by the surface film during summer, but not in autumn at lower temperatures. The first phenomenon should in the first place be due to the stratification of the water during summer, the last to the circulation in autumn and spring. During growth in the summer half of the year the growth of the crista cannot keep pace with what the stratification and the surface film demands if the animals should not be caught by the film. The swimming courses get too steep, resulting in contact with the film, and the final result is early death and shortlived specimens. On the other hand, in autumn and spring, when the cristæ for every week get shorter and shorter, the swimming courses for the low crested forms would theoretically become steeper and steeper, and the danger deriving from the surface film greater than in summer. When, nevertheless, this is not the case, this is due to the autumnal circulation of the water which is said to prevent the contact with the surface film. The final result should then according to WOLTERECK be that the animals because they are not caught in autumn by the surface film, get older, and that in spite of the fact that the assimilatory conditions, according to WOLTERECK, are less favourable at this period than in summer. —

It was in the lake of Frederiksborg Castle that the observations were made and with that lake in mind that the above-named passage was written. Especially with regard to this little lake the following remarks may be set forth.

The water of a lake with a depth of only 3—3½ m. is by no means regularly stratified during summer. During a calm period with high temperatures we can really find a temperature difference of about 2—3° C. at the surface and at the bottom. On the other hand in a country like ours where it almost always blows, the thermic stratification in so shallow a lake is often more than once a week almost totally obliterated, and the temperature, e.g. 18° C.—20° C., is the same at the bottom and the surface. To speak of a special annual period of stratification or circulation is in this case quite irrelevant. —

Further, WOLTERECK maintains that the assimilation conditions are worse in autumn and in spring than in summer. The real fact is that the Cyanophycé maximum begins in the last part of June, that it is extremely high during summer and the whole of the autumn, and that even during the whole of October the lake may be covered with a thick layer of Cyanophyceæ. If a gauzenet No. 20 is only for a minute drawn through the water, its inner side is coated with a thick layer of blue-green algæ. During the rest of the year the water layers are filled with enormous quantities of decaying Cyanophyceæ, detritus, skins of Cladocera etc. During the whole year in all water layers from the bottom to the surface, in all samples, minute algæ among which *Scenedesmus quadricauda* plays a very prominent part, are present in enormous amounts. The amount of food is always much greater than the consumers can use. The transparence of the water is never more than ½ m. commonly not 1 dcm. That in a lake of this nature the variations of food should in any way be able to influence the development of the buoyancy organs is impossible. In reality, here as everywhere, there is only one single outer factor which varies

regularly, and which indisputably causes a greater falling velocity for the organisms in summer than in winter, and that is the viscosity dependent upon the great annual regular variations in temperature.

In 1913 it was quite right that *D. cucullata* as a pond form had not hitherto been found in this country. This was, however, only due to the fact that I had not searched for it. This paper states that pond races of *D. cucullata* with typical round heads are for the greater part of the year present in a pond only 10 minutes from the lake by Frederiksborg Castle. Later on it has been found in several other ponds; mainly inhabited by *D. longispina* or *D. pulex*. Their number has always been small; the single individuals being found intermixed in the huge swarms of the above-named Cladocera. These pond races are unquestionably as common as in Germany. From Sweden they are well known through the explorations of LILLJEBORG (1900 p. 132).

If now we take into consideration the fact that with regard to the lake by Frederiksborg Castle we can only with an extremely large, but quite unknown, number of exceptions, speak of a period of summer stratification and spring and autumn circulation, that the plancton quantities and amount of detritus is enormous at least 2—3 months after the decrease of the crista, and that roundheaded pond races also occur in Denmark, it will be understood, that all the deductions with regard to the behaviour of the Cladocera in relation to the surface film in the lake by Frederiksborg Castle really rest on air. When we further remember that the deductions relating to the behaviour of the Cladocera to the surface film, as far as I can see, are all based upon the observation just in this single lake, it will be understood that the scientific value of all that part of WOLTERECK'S work sad to say is very strongly reduced.

That WOLTERECK'S suppositions are highly improbable is best perceived from the following fact. As the large maxima of *D. cucullata* always occur at the highest temperature, it is rather difficult to understand how the maxima should be developed, if all females, as soon as they had produced one or two eggsets, should be caught by the film and then die; moreover, it would not be easier to understand if the enormous decrease in number in the autumn should appear simultaneously with the time when the surface film owing to the circulation of the water and in spite of the steeper courses (more rounded heads) no longer represented any danger.

In this connection it must also be remembered that it would be a very dangerous matter on the part of the animals to use just the prolongation of the main axis as a means to escape the danger from the surface film. For it may be regarded as beyond all doubt that, all other things being equal, the forces exerted by the surface film are proportional to the line of contact. The biology of freshwater insects shows this conspicuously.

Also with regard to this part of the explorations in his last work (1920) WOLTERECK has added no new facts either with regard to the surface film or with regard to the thermocline: pp. 52—53 are only a repetition of pp. 522—523 in 1913.

The real facts are as follows. The duration of the life of the individuals is unquestionably much shorter during summer than during winter; in this sense the summer individuals are much younger than the winter animals which live more months than the summer individuals live weeks. In the weeks a summer daphnia lives, it commonly does not reach so large a size as a winter daphnia, which may live 6—7 months. This is not, as WOLTERECK seems to suppose, due to the fact that the summer daphnia, having passed about 7 moults, are caught by the surface film whereupon they die.

Most probably the summer and winter daphnia pass through the same number of moults but whereas the moulting processes in the first-named is begun and finished during a few weeks, in the last-named it is prolonged over 6—7 months; between the moults of a summer daphnia there are only 1—2 days, between those of a winter daphnia there may be several weeks. Whereas my vessels during summer contain innumerable daphnia skins, from my Daphnias taken in in November and living during the whole winter, in my aquaria at temperature near zero I only find very few.

WOLTERECK most probably comes to his supposition because all these summer daphnia commonly only possess 1—2 eggs. As far as we know, a moult always precedes the entrance of the eggs into the brood-pouch; therefore when we know that the first egg-set in a *D. cucullata* at all seasons is commonly only 1—2, and we find very high egg-sets in autumn and especially in spring, it is indeed tempting to suppose that when the Daphnia in summer only carry 1—2 eggs, then these summer-daphnias are all primiparæ and mainly die out as such. Here, in my eyes, is the chief fault on that point. During summer the moults follow each other very rapidly; the total amount of egg material which a summer daphnia can produce during life is split up into a large number of small egg-sets, all being only of 1—2 eggs; in the winter daphnias, after a resting period during which the animals only very rarely moult, it is produced in a few very large egg sets.

The Daphnias which WOLTERECK finds in the surface film of the lake by Frederiksborg Castle may have had as many moults as a winter daphnia which has lived for months, and may be very near the normal limit of their life time.

When WOLTERECK finds that the animals caught by the surface film have shorter cristæ than the young animals below it, this is only because he visited the lake at a time when the shortening of the cristæ had already begun. It is further in accordance with the fact which we observe every year in our aquaria, that the animals caught by the surface film live here for days, and when caught produce their young, which are not caught and stand in swarms a little below the surface.

The phenomenon, that some of the Plancton daphnids are in some lakes caught by the surface film, has nothing to do with the length of the crests or with periods of stratification and circulation. It is due to a combination of different facts of quite another kind: a special structure of the skin, the enormous oil-production in the said lakes. The surface film itself has not the slightest selective

influence upon the length of the cristæ, the more or less steep courses of the swimming tracts and very little upon the length of the life of the Cladocera.

III. The Bouyancy-Organs and the Nannoplancton.

The function of all buoyancy-organs as "Horizontalisierung und Steuerungsorgane" is, however, according to WOLTERECK, not only to prevent the organisms from coming into contact with the surface and bottom, it is in the first place to keep the organisms in quite distinct waterlayers, in which, owing to WOLTERECK, those organisms which form the nourishment of the Daphnids are to be found. In 1908 (p. 871) WOLTERECK has shown that probably the nourishment of the Cladocera mainly consisted in very minute algæ belonging to the so-called nannoplancton. In 1913 (p. 521) he says that according to explorations carried on from the Institut in Leipzig (Zugersee, Mansfeldersee) this nannoplancton shows a conspicuous zonal stratification during summer; during winter the distribution is homogeneous; the stratification of the nannoplancton begins simultaneously with the temperature stratification of the water, viz. the development of the thermocline. Just at that time all the buoyancy organs are developed. Now, according to WOLTERECK, the main significance of all these organs is to keep the animals "ständig in ihrer Nahrungsschicht". This nannoplancton according to the explorations, is said to carry out regular day and night wanderings; these wanderings again cause the regular wanderings of the Crustacea.

The "horizontalisierung" of the swimming courses is in the first place attained by means of the compounded eye, which, in the Cladocera, is to be regarded as a photostatic organ. The light causes a stronger motion, and forces the animal to take up a constant position in relation to the vertical. When a certain light intensity is reached, its influence causes the upward-directed motion to be altered as much as possible into a horizontal one; for the light forces the animals partly always to keep their dorsal side towards the light, always coming in from above, partly reflectorically to lower the head. The mechanism of the eye has been thoroughly studied; through these valuable studies a great step forward has unquestionably been made towards the understanding of the anatomy and physiology of the eye of the Cladocera.

According to WOLTERECK the light, by means of the eye, acts reflectorically horizontalising on the locomotion. This effect which is always present during day is then supported by the "Steuer- und Stabilisierungsorgane". During night it is only these organs which keep the swimming courses horizontal. This requirement must be fulfilled because the nourishment, the nannoplancton, during summer stands in special strata to which the Plancton daphnids are able to adjust themselves by means of the development of the buoyancy organs during summer.

When WOLTERECK published his mainwork in 1913 he based the picture he gave of the position of the nannoplancton mainly upon the just published studies of his pupils DIEFFENBACH and SACHSE. These studies were all only carried on in

ponds with maximal depths of only 1—1½ m., further, only upon Rotifera. The young men arrived at those results which WOLTERECK was to use, (1) The quantity of nannoplankton directly determines the quantity of zooplankton. (2) It is the nourishment which to a very high degree influences the body form of the Rotifera (“Die Annahme das verschiedene Aussehen der Rädertiere sei von der Tragfähigkeit des Wassers abhängig ist die Grundlage entzogen (1912 p. 21); für die Zyclomorphose ist einzig und allein die schwankende Ernährung verantwortlich (1912, p. 22). (3) The distribution of the pelagic Rotatoria is to the highest possible degree dependent on the position of the nannoplankton.

Especially when we remember that the depths of those watermasses in which these explorations have been carried on do not reach more than about 1—1½ m., i. e. not much more than the depth in a large aquarium, it will be understood that the young men have had the right localities for their studies relating to the scope of the buoyancy theories. What is necessary is only that the right people set to work! How a scientist can imagine that outer conditions, changing from day to day in these localities with their enormous variation in nourishment, in which every heavy rain and every summer breeze is able to set almost the whole water mass in circulation, should be able to have any form-changing influence upon the organisms, is difficult to understand. This especially holds good for the larger ones with their own high locomotoric motion. Nevertheless WOLTERECK used the explorations of the young men carried on upon pond rotiferes as proofs of his theories relating to lake daphnias, their position in their waterlayers, their cyclomorphosis, its origin and its significance. In the following years 1912—1920 many authors have dissented from the abovenamed three assertions.

However, WOLTERECK based his theory with regard to the position of the nannoplankton not only on the paper of DIEFFENBACH and SACHSE, it was also based on the hitherto unpublished explorations with regard to the relations between nannoplankton and the so-called Netzplankton, carried on at the initiative of Proff. CHUN and WOLTERECK. These papers were published in 1914. LANTSCH has studied the relations in the deep Zuugersee, COLDITZ in the shallow Mansfeldersee (7 m.). In his next work (1920) WOLTERECK (p. 53) writes: “Später wurde aber durch die Leipziger Arbeiten von SACHSE, DIEFFENBACH, LANTSCH und andere Arbeiten (I suppose COLDITZ) nachgewiesen dasz jene kleine Nähralgen im Sommer auf bestimmte Wasserschichten beschränkt sind. Infolgedessen giebt es in jedem See bestimmte “Nahrungsschichten” oder »Wohnschichten« für die einzelne *Daphnia*- und *Bosmina*-arten.”

In my eyes both these sentences are absolutely wrong. WOLTERECK has used the results of his pupils in quite an unallowable manner, and more than that, he has suppressed the earlier studies of RUTTNER which gave results that were not in accordance with those “facts” which Woltereck was to use for his theory. Before elucidating this, we may pay attention to the manner in which the term nannoplankton is used by the freshwater planctologists.

The term nannoplancton was first used by LOHMANN (1909 p. 201) to point out "jene kleinsten Auftrieborganismen die uns im Wesentlichen erst durch die Fangapparate der Appendicularen und die Zentrifugierung kleinster Wassermengen zugänglich werden."

In quite the same manner RUTTNER (1914 a. o.) used the term for the minute flora and fauna of the Lunzerseen. Later authors have quite forgotten the original meaning of the term, and use it as a substitute for the old term phytoplankton. Of COLDITZ's 17 species, 11—12 belong to the old term phytoplankton, of LANTZSCH's 29, about 24. COLDITZ (1914 p. 581) says expressly that all typical pelagic *Dinobryum* species, *Peridinea*, *Ceratium*, all Plancton diatoms, *Melosira*, *Asterionella*, *Tabellaria*, *Fragillaria* also belong to the category "Zentrifugen"- or nannoplancton¹⁾. Further, it must not be forgotten that when WOLTERECK's pupils want to use the term as a substitute for the term phytoplankton, they seem almost quite to have overlooked a very thorough exploration of the vertical distribution of the phytoplankton in the Zürichersee carried out by LOZERON (1902). Even if COLDITZ and LANTZSCH both cite LOZERON in their list of literature none of them take the slightest notice of his results. It must be pointed out that more than ten years earlier LOZERON p. 29 arrived at similar results as the two last-named authors. The phytoplankton is stratified according to the different species. On calm days *Clathrocystis* and *Anabæna* have their maxima directly at the surface; *Ceratium* and *Peridinium* from 0—30 m. and this is also the case with *Chlorophyceæ*; most of the other species diminish in number from 0—15—30 m. Only *Oscillatoria rubescens* has its maximum at 13 m. His chief result is that the phytoplankton is distributed mainly above the 50 m. curve.

It must be emphasised that if the term nannoplancton is used in the way it is by WOLTERECK's pupils, the difference between this term and the term phytoplankton is extremely small. —

When I doubt at present that the nannoplancton as LOHMANN thinks plays a similar role in the lakes as in the sea, it is owing to the following considerations. In very many of the larger lakes we do not find the alga material from which those strata of moving spores must develop. The home of most of the locomotive spores forming algæ is not to be found in larger lakes, especially not in Alpine lakes with cold water. Their home is to be found in ponds. The number of species growing in the littoral region of the lakes is never so large as in ponds; most probably also the period in which the species throw their spores here is much more restricted. Furthermore it may be regarded as beyond all doubt that the nannoplancton in Alpine and Arctic lakes plays a very inconspicuous role. With regard to the Davosersee SUCHLANDT (1917 p. 45) comes to the result that the nannoplancton only plays a role in the household of the lake from July to September and that the rest of the time it is very insignificant. From BACHMANN's explorations of the algal flora of Greenland (1921 p. 167) we are mainly entitled to expect that future explorations will give the same result.

¹⁾ The two terms are interchangeable (viz. LANTZSCH 1914 p. 689).

If we further remember that almost all the many hundreds of peculiar extremely small organisms, especially Chlorophyceae, Flagellata, Desmidiaceae a. o. studied during decennaries by a series of eminent algologists (CHODAT, LEMMERMANN, WEST, LAGERHEIM, BORGE a. o.), and on which the pupils of WOLTERECK have not bestowed the slightest notice, are almost all only found in ponds and ditches and only very few in lakes, we are entitled to suppose that the term nannoplankton, if used for freshwater, is more justifiable for the plankton of small freshwater bodies than for the large ones. We will return to this point later on.

All in all the term nannoplankton in larger lakes is to a very high degree restricted to the *Cyclotella*. As far as we have hitherto known these play a prominent part in the Alpine lakes; in the shallower Baltic lakes, with their great amount of organic matter, they do not seem to play such a prominent role; perhaps their significance here may be underrated.

At our present stage of knowledge it must be emphasised that if the term nannoplankton is to be used for a special part of the plankton of the lakes, this is only possible if we replace the term phytoplankton by nannoplankton; and it is just this that WOLTERECK's pupils have been forced to do. And, in other words, this means that, in all his speculations with regard to the relation between the position of the Cladocera in the waterlayers, their wanderings, and the significance of the buoyancy organs, on the one side, and the nutritive material, its position and wanderings on the other side, Woltereck is operating with a quantity the significance of which as nutriment may be regarded as highly problematic. We shall later on see that this really is rendered more than probable by NAUMANN.

As far as I can see RUTTNER is the only scientist who has studied the nannoplankton in a series of papers, in the same locality, regularly and with the best scientific methods and that just in the sense of LOHMANN. He is the only person who is able to have any opinion with regard to its wanderings and the relation between it and the zooplankton, and just he has in the most peremptory manner expressed himself against the main points in Woltereck's hypothesis, namely that the nannoplankton carries on regular day and night wanderings, and that these wanderings again cause the regular wanderings of the Cladocera. Of these papers by RUTTNER (1909 p. 174; 1914 p. 518; 1914 p. 3; 1914 p. 273) WOLTERECK has not taken the slightest notice in his main work (1920). RUTTNER's main results given 1914 a (p. 11) are that in the Lunzerseen "eine Verticalwanderung beim Nannoplankton ebensowenig stattfindet wie beim übrigen Phytoplankton". He further maintains "dasz von einem Zusammenhang von Vertikalwanderung der Tiere und vertikaler Verteilung der Nannoplankton nicht die Rede sein kann. Aber auch abgesehen von der Vertikalwanderung scheint mir die Bedeutung der Nahrung für die Verteilung der Zooplankton in den oberen Wasserschichten nicht allzu gross zu sein. . . . Auch in vertikaler Richtung ist es schwer Beziehungen zwischen den Verteilungsbildern beider Planktongruppen zu entdecken." RUTTNER maintains that above the thermocline the phytoplankton is regularly distributed, whereas the zooplankton

shows "die prägnantesten Verteilungsbilder". Also below the thermocline it is impossible to find any connection between the distribution of zooplankton and phytoplankton. Quite correctly RUTTNER points out that the phytoplankton can only then get significance as a nutritive factor "wenn die im Wasser vorhandene Nahrungsmenge im Verhältniss zur Individuenzahl der Konsumenten ein gewisses Minimum erreicht hat." This phenomenon, according to RUTTNER, seems only rarely to occur in the superior waterlayers.

In 1914 c (p. 327) RUTTNER further deepens the above named assertion when he says: "Bei einem Überschuss von Nahrung wird aber die Verteilung der Tiere von ihrem Einfluss unabhängig sein." He points out that already BURCKARDT a. o. have remarked that "ein bedeutender Einfluss dieses Factors in den bisher untersuchten Seen unwahrscheinlich ist." He maintains that in the Lunzerseen he has never found any correspondance between the distribution of zoo- and nannoplankton and that DIEFFENBACH'S experiments in the distribution of the nannoplankton to seek the main cause of the diurnal vertical wanderings of the phytoplankton may be regarded as "entschieden verfehlt". He seeks the main factors of the vertical wanderings partly in mechanical, partly in biological factors: temperature, but quite especially light. With LOEB he is inclined to see in phototactic "Reizbewegungen" one of the main causes of the diurnal vertical wanderings. ROBERT also comes to quite the same result (1921 p. 67) with regard to the lake of Neuchâtel. On p. 65, however, he remarks that during the strongest development of the phytoplankton "les espèces profondes" (*C. strenuus*, *Sida*, *Daphnia*) are found near the surface and asks if the nutritive conditions, which may be more convenient than in the depths, cause the phenomenon.

If now we remember that RUTTNER'S explorations are carried on in a clear Alpine lake, and that these explorations could not possibly have been unknown to WOLTERECK, it is in my opinion quite unintelligible how he could suppose that just in the shallow Baltic lakes e. g. that of Frederiksborg Castle the amount of nourishment even if it in any way could influence the presumed wanderings of the Cladocera, also in any way could influence the development of the buoyancy organs. In this connection it must not be forgotten that these wanderings in the Baltic lakes are most probably of relatively slight importance here; the transparency of the water being very small in most of them the animals live almost the whole year round in a medium which in very many cases must if anything be designated as bouillon, very different from that of the clear Alpine lakes where these wanderings play a very prominent part in the life of the animals, see BURCHARDT (1900 p. 248), STEINER Luganersee (1912 p. 59) a. o.

The total suppression of RUTTNER'S results especially in 1920 is one of the gravest objections which can be advanced against the whole working method of WOLTERECK. — As mentioned above, WOLTERECK maintains that the main significance of the buoyancy organs is to take care "dasz die Tiere ständig in ihre Nahrungsschicht bleiben". As the nannoplankton depends upon variations in light, ac-

ording to Woltereck is supposed to undertake regular vertical wanderings, WOLTERECK is of opinion that the peculiarities of the wandering of the Cladocera may be regarded as "Folgeerscheinung des Auf- und Absteigen ihrer Nahrung" (1913, p. 521).

In 1913 WOLTERECK expresses himself very cautiously, in 1920, however, more peremptorily. P. 55 he says: "When die lichtempfindlichen Nahrungsorganismen darauf ebenso reagieren wie die Cladoceren so bleiben die letztern immer dort, wo sie sein sollen, nämlich im Bereich ihrer Nahrung. . . . Die Unterschiede von Tag, Dämmerung und Nacht veranlasst die sogenannten Vertical-Wanderungen der Cladoceren und gewissen, beweglichen Nannoplanktonalgen." The main results of all buoyancy organs are therefore said to be "die Schwimmbahnen abzufachen": to produce: "eine Beschränkung der Tag und Nacht Wanderung auf schmalere Wohnschichten." The first condition for this supposition is that the said Cladocera really are to be found in these strata of nourishment. Therefore WOLTERECK is forced to write: "Die Beschränkung scheint dem sommerlichen Vorkommen der Nähralgen zu entsprechen". To this supposition upon which depends WOLTERECK'S whole theory with regard to the buoyancy organs as "Steuer- und Stabilisierungsorgane" W. has, as far as I can see, never himself contributed anything. His supposition is in contradiction to the earlier explorations of RUTTNER which W. ignores, but based upon those of his pupils, firstly on those of DIEFFENBACH and SACHSE, carried on in ponds, and therefore rather valueless for the lakes, and secondly on those of LANTSCH and COLDITZ. The papers of these young men both show into what an unpleasant situation they have got. Both contradict themselves in their main results, and the more they approach the end of the exploration, the more obvious is it that the desired result cannot be produced.

For Mansfeldersee COLDITZ (1914 p. 606) writes: "Unberührt von jeder Einwirkung des Lichtes blieb die Verteilung der Nahrung. Die Z-Planktonen (= nannoplankton) lieszen keine Spur von Wanderungen zu erkennen und demnach können sie als Ursache für die tägliche Verteilung des Netzplanktons in diesem Gewässer nicht in Betracht kommen. Es steht in direktem Gegensatz zu den Befunden DIEFFENBACH'S in Teichen."

The explorations of LANTSCH (1914) with regard to the so-called nannoplankton of Zugersee (depth 198 m.) are the only more thorough ones carried on upon the vertical distribution in lakes which we possess. The main results are the following.

LANTSCH (1914 p. 689) writes as follows: "Das Nannoplankton der Zugersees zeigte im Sommer und Herbst eine charakteristische Schichtung." This is in accordance with what WOLTERECK needed. When next, however, it must be admitted that the lower limits for the nannoplankton go down to "rund" 80 m., and that the "mittlere Tiefe" is only 85 m., further, that the layer 50—80 is mainly inhabited by *Chroococcus*, *Gomphosperia* and *Cyclotella*, and that the *Flagellata* "are limited" to the whole water layer from 0—50 m. it is difficult to understand how WOLTERECK can be content with the result. What W. wants is well marked strata, with

a copious amount of nourishment, limited on both sides by others with small amounts i. e. such in which the animals cannot live or can not propagate. These have never been pointed out. LANTSCH (1914 p. 676) has quite correctly understood this; he writes that in deep lakes there will always be a waterlayer of more than 50 m. at the disposal of the zooplankton. His main result is that there is no conspicuous quantitative difference between the nannoplankton during night and day at the surface. With regard to the Copepoda he says (p. 670): "Die von DIEFFENBACH auch für Seen fest ausgesprochene Ueberzeugung, es möchte sich der Andrang der Copepoden auf Ansammlungen von Zentrifugenplankton an der Oberfläche zurückführen lassen, kann ich nicht bestätigen". With regard to the Rotifera he shows that the maxima for the nannoplankton and Rotifera do not coincide. *Flagellata* and *Cyclorella* are found from 0—1 m., the maxima of the Rotifera from 2 m. The flagellates as well as the Rotatoria carry out regular wanderings: "Nur liessen sich in Zugersee die Ortverschiebung bei der Gruppen nicht auf einander zurückführen, die Amplituden der Wanderungen sind nicht die gleichen (LANTSCH 1914 p. 689). Wir kommen zu dem Satze, das in tiefen, klaren Seen der die Vertikalverteilung regelnde Faktor das Licht ist und eine direkte, unmittelbare Abhängigkeit von Nannoplankton nicht wahrscheinlich ist (p. 686)". With regard to the Cladocera it is of course rather difficult for LANTSCH to give his mentor the desired main result. On p. 678 he must, however, confess with regard to the development of *Daphnia* and *Bosmina*: "Jedenfalls kann ich mich nicht entschlieszen sie allein vom Zentrifugenplankton abhängig zu machen. . . . Die physicalischen Faktoren scheinen bedeutenden Einfluss zu besitzen", i. e. just the result at which OSTWALD and I have arrived.

It is difficult to understand how WOLTERECK can claim that these papers have shown that the nannoplankton is bound to special water strata and that the species of *Daphnia* and *Bosmina* in every lake have their special strata of nourishment (1920, p. 53). Not in a single lake has this assertion been corroborated. When LANTSCH (1914 p. 676) tries to comfort his mentor with the hope that in the relatively shallow Baltic lakes with depths about 40 m. the conditions may be different and more in accordance with WOLTERECK's needs, it must be remembered that it is highly improbable that just in these lakes with their enormous amount of phytoplankton we should find special strata of nutriment in which the Cladocera were forced to live and adjust themselves morphologically. Where are the Baltic lakes or lake ponds where "zonar begrenzte Nahrungsschichte" have been pointed out? (LANTSCH 1914 p. 677). It may further be pointed out that also other explorations have never been able to corroborate the suppositions. In the lake of Zürich HEUSCHER (1917 p. 178—183) as far as I can see, has found no concordance between stratified producers and stratified consumers. HARTMANN also comes to a quite similar result in his papers relating to the cyclomorphosis of the Cladocera and Rotifera (1915 p. 507 and 1920 p. 300).

As early as 1918 OLUFSEN, in one of the most thorough papers relating to plankton organisms which we possess, has dissented from Woltereck's theories;

I refer the reader to OLUFSEN's work especially to pages 411—417. The objections are quite the same which have been stated here. With regard to the nourishment as a significant factor for the development of the buoyancy organs he thinks "Dasz die Verteilung der Nährsalze während der verschiedenen Jahreszeiten (mit der der Planktoncladoceren) übereinstimmt, wie WOLTERECK es betont, ist bis auf weiteres eine unbewiesene Annahme"; WOLTERECK's narrow strata of nannoplancton do not exist. With regard to the proposed selective action of the surface film OLUFSEN quite correctly says: "Stände die Entwicklung der Richtungsorgane in irgend welchem Zusammenhang mit der Selektionswirkung der Oberfläche, so wäre es unerklärlich, weshalb die Temporalvariation gerade bei einer Temperatur von 14—16° C. auftreten sollten, was sowohl W.-L. als WOLTERECK gefunden haben." With regard to the significance of the thermocline OLUFSEN has also great hesitation; he shows that in August he has found *D. hyalina* much more numerous below than above the thermocline.

Of special interest is the following remark (p. 415) which entirely coincides with what I wrote at pag. 173: "Vor allem glaube ich, dass WOLTERECK allzu sehr die Bedeutung der Ruhestellung und den vollständigen oder teilweisen Rückgang zu dieser zwischen den Schwimmstößen unterschätzt hat." He points out especially in contradistinction to WOLTERECK that the spina especially in the position of repose has great significance in diminishing the rate of sinking. He sums up his views with regard to WOLTERECK's theories in the following words: "Für diese Temporalvariationen liefert die Woltereck'sche Theorie also keine Erklärung. Sie stehen im Gegenteil in entschiedenem Widerspruch zu derselben." — This view entirely coincides with mine.

It will most probably now be understood that when WOLTERECK (1920 p. 53) maintains that in every lake there exist distinct strata of nourishment or strata of habitat for every ("für die einzelne") *Daphnia* or *Bosmina* species, this conclusion is irreconcilable with the real facts.

Then it will, however, also be understood that one of the main points of WOLTERECK's interpretation of the buoyancy organs as organs by means of which the organisms should be held in special strata of nourishment (WOLTERECK 1920 p. 69) is, so to speak, reduced to nothing. On the other hand, if we take our stand on the buoyancy theory, it cannot be denied that W. has to a very high degree, especially with regard to the *Bosmina* body, contributed to solve the question of how the organisms adjust themselves to the augmenting rate of sinking during summer; and limnology will then always be in great debt to him for what he in this way has yielded.

IV. The explorations of NAUMANN a. o.

During the last few years a series of papers have appeared all relating to the fresh water ponds and ditches. Many of these papers have principally shared practical

views; nevertheless many of the results have scientific value and the authors have taken decided ground just with regard to the questions which have occupied us here. We will here shortly deal with those of SCHAEDEL, WUNDSCH and NAUMANN.

SCHAEDEL (1917 p. 404) has correctly seen that the term nannoplancton cannot be used as has been done by COLDITZ and LANTSCH. In his valuable papers he has tried to study the relations between the producers and the consumers of the pond plancton. The term nannoplancton is only used for the most minute organisms of the centrifuge plancton; the rest of the old term phytoplankton is correctly divided in Sieb or Netzplancton and Centrifugeplancton.

The explorations show firstly that in ponds we really can speak not only of a zentrifuge plancton but also of a real nannoplancton; this is in entire accord with the earlier explorations of CHODAT, LEMMERMANN, WESTS a. o.

SCHAEDEL has further seen that there is agreement between the curves of the nannoplancton and the zooplancton, that the nannoplancton in the ponds stands in special strata, and that these coincide with those of the zooplancton (in accordance with point 1 (pag. 188) of the results of DIEFFENBACH and SACHE). Further, he correctly points out that in this respect there are great differences between the relations in ponds and in lakes; according to him this is fully intelligible. In ponds the "Wohnverhältnisse in der Verticale" are "enge und gedrängte", "die Transparenz wird herabgesetzt durch die grossen maximalen Entfaltungen der produzierenden Zentrifugenplanctonten" (p. 558). On the other hand in the deep Alpine lakes the space is much more extended; the transparency is much larger and is only slightly weakened by the influence of the zentrifuge plancton; the single planctonts spread vertically to considerable depths.

Of special interest is the fact that SCHAEDEL has shown that the temperature has only influence in the colder parts of the year; not so much in the summer half of the year; when the optimum is reached, other factors, light etc., have a greater influence.

From autumn to the middle of April "bewirken schon ganz geringe Unterschiede der Temperatur eine Zu- resp. Abnahme der Produzenten und damit verbunden der Konsumenten. Die Temperatur hat, nachdem sie bis zu einem gewissen Betrage gestiegen ist, keinen Einfluss mehr auf den Cyclus der Planctonten (Optimalbereich der Temperatur). Erst wenn sie im Herbst wieder endgültig unterhalb dieses Bereiches angekommen ist, wirkt weitere Temperaturabnahme vermindern auf die Planctonproduction ein." Later on WUNDSCH (1920 p. 3) has called this sentence "die Formel von dem optimalen Temperaturbereich für die Massenentwicklung der tierischen Planctonten"; perhaps one of the most significant results of the hydrobiological explorations of recent years.

In an excellent paper by WUNDSCH (1920 p. 1) based upon his own earlier and Dr. MARIA PAULY's thorough papers (1919 p. 210) and (1919 p. 408), WUNDSCH has elaborated the results of SHAEDEL.

His explorations have in the first place practical purposes and have been carried on in very shallow fishponds; in summer often shallower and to a high

degree covered with vegetation; the plancton has been taken when wading in the ponds; every tenth day 20 times five liter taken in with a bucket has been thrown through a planctonnet.

Many of the problems which have a purely scientific interest cannot of course be advanced in ponds of this structure and in this manner. This is quite clear to WUNDSCH; we get no information with regard to cyclomorphoses, vertical wanderings etc., but he has succeeded in very shallow water in a very convincing manner in showing the relations between temperature and the amount of producers and consumers of the plancton. Of the greatest interest is the fact that the temperatures are not taken one single time in the day, but by "selbstregistrierende" thermographs "die es ermöglichten, die Durchschnittsp. des Teichgewässers täglich auf Grund des wahren Tagesdurchschnittes festzulegen." Owing to this WUNDSCH is able to show above all that the temperature curves given by DIEFFENBACH have only a very slight scientific value; they are unsuitable to show that temperature has no significance as an outer factor for the consumers and cannot be used to point out the relation between temperature, producers, and consumers.

In contradiction to the earlier authors DIEFFENBACH, SACHSE, COLDITZ, LANTZSCH and SCHAEDEL, his main result is that the amount of zooplankton (Netzplancton) "an geeigneten Örtlichkeiten" may be dependent upon variations in temperature and not on the amount of producers. According to him (1920 p. 43) the influence of the temperature is the primus motor by means of which the utilization of a specific supply of nourishment at a given time is either made possible or prevented. Variations in temperature can only influence the amount of the zooplankton at the period when the amount of nourishment is simultaneously in optimum and therefore is persistently constant. The more a volume of water may be regarded as a pond or ditch the more will the variations in temperature influence the zooplankton. Owing to the papers by the pupils of WOLTERECK, WUNDSCH is inclined to suppose that in the large and deep lakes with their more uniform temperature this should not be the case. Not knowing the papers of RUTTNER, WUNDSCH, I suppose, has overrated the significance of those of the school of WOLTERECK.

The observations of SCHAEDEL and WUNDSCH are in accordance with my own unpublished explorations of the pond plancton. That in many ponds there is a conspicuous agreement between the curve of the nannoplankton and that of the zooplankton is very pronounced. On the other hand I have also rather often got observations where this seems not to be the case. Especially in spring at a temperature of 12—14° C., huge maxima of perennial Rotifers are developed some weeks before the maxima of nannoplankton set in; we will elsewhere return to this point. It is highly probable that in volumes of water with a depth of one or two m. the different nannoplankton are mainly gathered in special strata owing to their demands for light, and further that organisms which prey upon them are really to be found in these strata. In bright sunshine I have from my boat often seen a foglike veil standing at a depth of $\frac{1}{2}$ m. below the surface layer of extremely clear water. The

veil was due to enormous amounts of *Ceratium hirundinella*. It is also a very common phenomenon to see clouds of *Chlamydomonas* standing spread over the lake forming green spots with clear water between; the spots are determined by the amount of light, again determined by the surroundings (trees etc).

On the the other hand it may be regarded as highly improbable that vertical wanderings in water volumes of so small a size and with such an inconspicuous depth should show any pronounced regularity; or that because the development of the buoyancy organs coincides with the increasing maxima of the nannoplankton it is a direct result of it, or that the organisms should be forced to develop organs the function of which should be to keep them in quite special strata. In localities of this nature their own locomotoric motion is most probably sufficient.

At all events it is quite unallowable to transfer the results of the explorations on the behaviour of the organisms in ponds to those of the organisms in lakes.

WOLTERECK's pupils have quite correctly understood this. LANTSCH (1914 p. 688) writes: "Wir dürfen Teich und See nicht one weiteres vergleichen". Nevertheless it is just this that WOLTERECK does, using the results of DIEFFENBACH and SACHSE and referring to the papers of SCHAEDEL and others.

During the last few years different authors (HARTMANN 1915 p. 436, 1920 p. 209 a. o.) have tried to find and bring into accordance with the buoyancy theory yearly variations in size and special body structures of pond organisms and of organisms from the bottom and littoral region (most of the *Ceriodaphnia*-species, *D. pulex*, *Acroperus*, *Camptocercus*, many Rotifera). The explorations originate from very small ponds and ditches, often in holes not much more than a few square meters in diam. I regard most of these attempts as very unfortunate. Even under life conditions of this kind we may really find localities where we can find typical cyclomorphoses, and where we are able to regard them as being in accordance with variations in outer conditions, especially of physico-chemical nature (LAUTERBORN: *Anuræa*), most probably not in amount of nourishment. In most cases this will not be possible. The scientists seem quite to have overlooked the fact that the great regularity in the surrounding medium characterizing the temperature, chemical composition, light, and viscosity in the large lakes is never to be found in ponds and ditches. A cold summer night can here suddenly produce temperatures near zero, heavy showers redouble the volume of the water in the course of a few days and simultaneously dilute it very considerably, and a drought period of only a few days let the whole volume of water disappear. That in a medium where the life conditions are of so small stability it should be possible to bring variations in outer form in accordance with the requirements of the buoyancy theory, or vice versa bring all fluctuations in accordance with variations in buoyancy conditions, temperature, nourishment, viscosity, light, number of generations, is an unscientific demand. Of course the variations in the rate of sinking even in the smallest volume of water also here govern the life and form of all free-swimming organisms, but they are here combined, counter-

balanced, supported or put out of question by so many always varying factors that it is only rarely possible to make anything of them.

To what preposterous results WOLTERECK's pupils come when the main stress is to be laid either upon inner conditions or upon nourishment KRÄTSCHMAR (1913 p. 49) gives a good example of. When the explorations upon *A. aculeata* in the one pond (that of DIEFFENBACH) give the result that variation in nourishment "einzig und allein für die Zyclomorphose verantwortlich ist", whereas in another pond it may clearly be shown "dass die Anuræen in ihrer Variationstendenz in keiner Weise durch Ernährungsverhältnisse beeinflusst werden konnte", he only divides the species in two subspecies: *A. aculeata variabilis* and *A. aculeata* Ehrbg., distinguished from each other mainly by their tendency to variation in accordance with variation in nourishment. When KRÄTSCHMAR, as further support of his systematic arrangement, maintains that in *A. aculeata* we find two sorts of resting eggs, one with spinose chitinous covering and one with a smooth covering, this is correct, but as far as I can see, KRÄTSCHMAR has not been able to show that the spinose egg regularly belongs to *A. aculeata* and the smooth one to a *aculeata variabilis*.

In the last few years explorations have been carried on in Sweden which are of the greatest interest for all questions treated in this paper. NAUMANN (1918—1921) has tried to show that the nannoplankton has by no means the great significance for the zooplankton hitherto supposed. He maintains "dass wohl in erster Linie eben der staubfeine Detritus nebst den Bakterien als die unter allen Umständen wichtigste Nährquelle des tierischen Limnoplanktons vom filtrierenden Typus (not robbers: *Leptodora*, *Polyphemus* and *Bythotrephes* of the *Cladocera*) aufzufassen ist". Most probably NAUMANN is right, and quite correctly he therefore concludes that the supposed dependence between phyto- and zooplankton does not exist. "Vielmehr sind nunmehr alle Schlüsse über die nähere Art der Abhängigkeit der Konsumption von der Production auf Grund von statistischen Untersuchungen als ganz werthlos zu bezeichnen. Es ist nämlich gar nicht der Totalgehalt der Nanno bezw. Ultraseston der dies reguliert. Vielmehr handelt es sich hier um die qualitative Sonderart um die wechselnden Nährwerthes des Sestons". NAUMANN maintains (1918 p. 39) that this holds good as well for the *Cladocera* (1.) in lakes characterised as "seichtere Gewässer nährstoffreicher Gebiete mit über 16° sommerlichen Mitteltp." as (2.) "in nährstoffarmen Gegenden der kalkarmen Urgebirge" and (3.) "in tiefere Gewässer ganz unabgesehen von ihrer geographischen Lage," in short, all lakes in which the relation between phyto- and zooplankton has hitherto been studied. In the first type the zooplankton is really dependent upon the phytoplankton "wenn auch oft in einer ganz indirekter Weise indem das Phytoplankton wahrscheinlich minder an und für sich als vielmehr als Detritusproduzent und zwar theils durch Production von in Wasser später aus flockenden Assimilaten theils aber auch erst bei ihren Absterben von einer grundlegende Bedeutung ist" (1918 p. 39). In Typus II the filtrate is "feinster Detritus; Gehalt an Algen bezw. Flagellaten mehrenteils sehr gering"; in Typus III

“besteht das nährende Filtrat aus einer quantitativ oft unbedeutlichen Kombination, von Algen bezw. Peritripton (= staubfeine Detritus)”.

From a purely limnological standpoint, and in accordance with the explorations of RUTTNER, NAUMANN is most probably right. In all our lakes the depth of which never exceeds 40 m., the water layers most probably the whole year round contain a constant excess of nutritive material. In the greater part of the year the material is mainly phytoplankton or derives from that, at certain seasons mainly detritus. Especially in spring the numerous rivulets and smaller streams carry enormous amounts of organic detritus into the lakes, especially where the drainage area is well cultivated; in early spring ice erosion and gales in our shallow lakes carry enormous amounts of dust fine detritus over the lakes. Before the ice melts, the surface is covered with a dark layer of atmospheric dust, Conifera pollen etc., which all sinks to the bottom; in May—Juni when the beech flowers, the surface of all lakes is for a short time yellow; all this material, even if some of it will for a short time be deposited in the littoral region, will be carried] out over the lake and as dust sink downwards through the plankton-harboursing water layers. It is a well known fact that the rivers push their water masses horizontally into the water layers of the lakes (“bataillière de la Rhone”). No one has studied the detritus amount in the middle of the water layers in larger lakes; irregularities with regard to the vertical distribution of the zooplankton may perhaps be referred to this phenomenon. At our present stage of knowledge we are inclined to suppose that especially in the larger lakes and most in the types II and III of NAUMANN the nannoplankton as nutriment really plays a very inconspicuous role in the life of the Cladocera. If this really holds good this, however, means, in other words, that all WOLTERECK'S deductions relating to the supposed fact that the Cladocera should be tied to special strata of nourishment are absolutely wrong. Whereas it might be supposed that the nannoplankton, owing to variations in light, was tied to special strata, this cannot be the case with the dead dustlike Peritripton. That this should make regular day and night wanderings is still more impossible. From this again results that the buoyancy organs cannot be regarded as organs by means of which the organisms try to horizontalize their swimming course, the reason of which in the first place should be to keep them in special strata of nourishment, moving up and down in accordance with the nourishment, the strata of which again are dependent upon differences in light conditions.

We should now expect that NAUMANN would draw these conclusions from his explorations; but this is by no means the case. To combine his own new valuable results with the earlier results relating to the interdependence of phyto- and zooplankton he has correctly seen is an impossibility. Nevertheless, in some series of papers he is inconsistent enough to maintain that the deductions of WOLTERECK are correct and seems to share his rather peculiar view, peculiar in relation to his own upon this point valuable explorations, that the buoyancy theory is not only superfluous but also absolutely wrong. This seems to be the

result of a whole series of papers. Here we will restrict ourselves to the following assertion (1924 No. 26 p. 5) relating to the paper of W. 1913. "Diese Arbeit hat auch der speculativen Schwebetheorie auf diesem Gebiet einen ersten aber auf einmal katastrophalen Grundschuss gegeben". Simultaneously with the pointing out of the fact that the nannoplancton has no significance as food for the Cladocera NAUMANN follows WOLTERECK in his view that the buoyancy organs may be regarded as means by which the organisms keep themselves in just those strata in which this nannoplancton lives, just that nannoplancton which, according to WOLTERECK, is the main food of the Cladocera, and more than that, according to him, through selection has influence upon the production of the buoyancy organs.

In a series of papers, from rather few observations and from the slightest possible stock of knowledge most of the phenomena related to those studied, without any deeper literary knowledge and totally lacking time enough more thoroughly to finish and think over the observations, NAUMANN has tried to press Nature into a series of highly artificial schemata which are unquestionably very valuable for all those scientists whose time is just as scanty as his own, whereas from a purely scientific point of view, as far as I can see, they have very little value.

Having now finished my critical examination of the literature after 1908 relating to one of the greatest chapters in limnology, I wish to conclude with the following remarks.

In my eyes the buoyancy theory as it was set forth in its fundamental lines in 1900—1910 is just as necessary now as then if we want to understand the biology and morphology of the plancton organisms of the freshwater.

Because it has been tried upon single organisms, removed from their natural life conditions, because the studies were carried on not from a biological but from a hereditary point of view, and last but not least because the students themselves were to a very great extent often very young men without deeper scientific education, and who only rarely continued their studies, it is intelligible that the theory during the last few years has fallen into discredit. Modern currents in limnology are far removed from the natural base of these studies.

Remarks on Heredity.

In the foregoing I have tried to show that the four *Daphnia*-species treated in this paper may be regarded as a developmental line beginning with *D. magna* living in warm drying up pools rich in organic matter, and finishing with the pelagic *D. cucullata* inhabiting the pelagic region of larger lakes. This view of our *D.* species has already been mentioned (1904—1908); it has been adopted by WOLTERECK (1919), but, as far as I know, no one has tried more thoroughly to study the species in Nature from this point of view. The classification of the Daphnids in P. Daphnids and M. Daphnids (WOLTERECK 1919 p. 36) I regard as highly problematic. —

On page 154 I have supposed that the rising temperature subsequent to the improvement in climate after the Glacial Age was the direct external stimulant responsible for the occurrence of different form series of which several may be found in the fresh water plancton and among which that of the *Daphnia*-species is one of the most conspicuous.

This is only a further explanation of the admirable explorations carried on by EKMAN (1904) on the *Daphnia longispina* races in Sweden and especially in the Sarek-Mountains. —

EKMAN (1904 p. 127) considers the pond and pool form of *D. longispina* var. *rosea* the most primitive. From this form arose the var. *abbreviata*, a form specially adapted to arctic conditions. This form was again the starting-point of the progressive series *frigidolimnetica-microcephala-obtusifrons-galeata*, which all represent adaptations to a pelagic life, *frigidolimnetica* under extremely cold temperatures, the others under conditions less severe with respect to low temperatures. Var. *rosea* has also, however, through the variety *intermedia* and under less severe climatic conditions developed into pelagic races belonging to the varieties *longispina*, *lacustris*, *hyalina*. A similar mode of life has caused such a similarity in the forms of these two progressive series, although their origin was not the same, that they cannot be distinguished from each other. In the form var. *rosea* EKMAN shows that *D. longispina* still occurs as a pool form throughout Sweden and the Central-European plain and lower mountains; on the other hand the pelagic races adapted to special arctic conditions, as *frigidolimnetica* and *intermedia*, no longer occur, at any rate

in South Sweden and Denmark. In their place we find the forms deriving from them, var. *obtusifrons* and *lacustris*, together with those deriving again from the latter and adapted to higher temperatures, viz. *galeata* and *lacustris*. In Denmark these races are by far the most predominant. I further refer the reader to Plancton Investigations (1908 p. 127). I only regret that the numerous German explorers have taken very little notice of the very valuable researches of EKMAN. If they had done so, we should have been able to draw up the form series with much more certainty through the whole of Europe than now. —

In the variety *rosea* and probably under the form *abbreviata* *D. longispina* was one of the first forms which took possession of our pools and small lakes during the melting period of the ice. When the pelagic regions in larger lakes became suited to a permanent pelagic fauna, *D. longispina* through the *frigidolimnetica*, *microcephala-galeata* series was one of those small water forms which first took possession of them. Through the form *intermedia* the *rosea-hyalina* series supervened, perhaps somewhat later. With the improvement of the climatic conditions var. *frigidolimnetica* and var. *intermedia* disappeared, first giving rise to the two series *microcephala-galeata* and *lacustris-hyalina*. Common to them all were the comparatively slight seasonal variation, small A, peculiar head, relatively short clumsy shape, large eye and short spina, a greater transparency and somewhat longer spina than the pond forms. The colonies both in lakes and ponds formed ehippia every year, and any appreciable local variation in the colonies in the different lakes hardly occurred.

Before entering deeper into the question of how the single units in the form series must be interpreted, I take the liberty to set forth some ideas that have occurred to me during my work with this subject and which have occupied me for several years.

In addition to the well known often mentioned objections to the mutation theory e. g. that the very complicated shades and markings on the wings of the Lepidoptera and the phenomena of mimicry combined herewith, further the co-adaptions, the correspondence (the mutual adaptation) between the length of the tubes of the flowers on the one side and the length of the proboscis of insects and the beaks of colibries on the other, further between the bow and "Schrilleiste" of the music-making insects etc. cannot be brought in accordance with the mutation theory, it has often been emphasised that the so-called form series also cannot be interpreted in this way. These form series may be classified in three groups: 1. The geographical ones, 2. the geological ones and 3. the biologicomorphological ones.

It cannot be denied that the deeper we enter into the mutual relationship of the organisms the more significance do these form series acquire. Further that a good deal of the systematics of birds, of insects, especially Coleoptera and Lepidoptera, of the mammalia, of Molluscs and also of the Protozoa (Radiolaria) operate with the term form series as an established fact. It seems as if the species arrange

themselves in time and space in series of forms where the single units in accordance with small variations in outer conditions through small morphological variations are arranged in chains where the single links are joined to each other and imperceptibly pass over into each other. As CRAMPTON (1916 p. 31) correctly says: "The role of the environment is to set the limits to the habitable areas or to bring about the elimination of individuals whose qualities are otherwise determined — that is by congenital factors". — Quite correctly RENSCH (1926 p. 254) says: "Es mag an dieser Stelle betont werden, dass derartige Rassenkreise im ganzen Tierreich, auch bei marinen Formen, vorhanden sind; . . . Wie die moderne Systematik der Vögel zeigt, sind im übrigen solche Rassenkreise nicht etwa gelegentliche Fälle, sondern umgekehrt die nicht geographisch variierende Arten seltene Ausnahmen." Especially the last Congress of Ornithologists in Copenhagen (1926) showed how correct this assertion is.

1. As examples of the geographical form series or "Rassenkreise" we will only mention the following from Zoology: (that similar form series are also known in the vegetable kingdom is a well known fact (vid. WETTSTEIN a. o.)). Thus the form series of land-molluscs on Celebes (SARASSIN 1898), of *Bulimiella* on the Hawaiian Islands (GULICK 1905), of *Cerion* on the Bahama Islands (PLATE 1907), of *Partula* on Tahiti (CRAMPTON 1916), of *Amphidromus* on TIMOR (HANIEL 1921), of *Achatinella* from the Sandwich Island Molokai (BORCHERDING 1906), of *Campylæa* from Central Europe (RENSCH 1926); the form series of Radiolaria (HAECKER 1909), of the Zebras of Africa (RIDGEWAY 1909), and (after HAECKER 1921) of different Coleoptera and birds (*Acanthis*, *Melospiza* a. o.).

2. That the species are arranged in form series not only in space, but also in time, is a well known often mentioned fact. Between such geological form series the best known are perhaps: the lower pliocene *Paludinas* from West Slavonia explored by NEUMAYR (1875) and those of *Planorbis multiformis* from Steinham studied by HILGENDORFF (1866; 1901).

3. The more the species and genera are studied morphologically and biologically the more evident it is that in the most different parts of the animal kingdom the units may be arranged in series of forms where the specific characters for the species and the genera present direction-determined continuity; these marks present themselves as increasing adaptations to modifications in outer conditions, deriving from variations in the mode of living tending in certain directions.

It may be presumed that the way in which variations in outer conditions influence the organisms is that a biological separation precedes the morphological one. The more the study of the biology of the organisms proceeds the more conspicuous is it that the species are split up in biological races showing no morphological differences. These biological variations are often geographically determined, produced by variations in outer conditions, mainly variation in nourishment, in the last few centuries often produced by man himself. It would take us too far afield if we were here to give examples; they may be found in almost every part

of the zoological literature from the last thirty years. I need only mention the biological variations of the Anophelines, the discovery of the races *misanthropes* and their significance for the disappearance of malaria over vast parts of its former area.

Owing to the excessive use of certain organs through vast periods of time, the organisms were modified morphologically. Even if I cannot fully sanction the view of NÄGELI that "das Bedürfnis nach einer neuen nützlichen Eigenschaft diese direkt bewirke" on the other hand I do not agree with PLATE'S (1913 b p. 501) sharp rejection of NÄGELI'S a. o. view. It must not be forgotten that living organisms are not machines, but that in every one, from the smallest Amoeba and up to the highest of the primates, there is a psychological force, incomprehensible and unintelligible, in my opinion, however, scientifically indisputable, just that force which separates the organic world from the inorganic. We can put an Archimedian screw in a jar, and it depends only on us, if the screw shall be used to empty the jar; and we can bring a horse to the jar, but if it will not, we cannot make it drink. It is this same force, common to all organic life, which governs or is a concurrent motive to the behaviour of the organisms, and therefore also to the different intensity and the manner in which the different organs of the organism are used. Dependent upon regular variations in the surrounding medium these results of pleasure and displeasure, causing exaggerated use or non-use of special organs, may often be the *primus motor* for morphological variation. It is just this psychophysiological aspect of all organic life which in many cases gives to Lamarckism its right and its preponderance over the doctrine of selection. It is as if almost all students of heredity so to speak in all their calculations have overlooked this one half of the whole organic world, that world which they are devoting their life to studying. Sooner or later the exaggerated demand for "exactness" and the disregard for all that scientific work which cannot be converted into columns of figures, will bring the study of heredity, taken in the widest sense of the word, to a stand-still.

It cannot be denied that it is tempting to interpret many cases especially relating to the metamorphosis of insects in the sense of NÄGELI. I take the liberty to point out a few examples from my own area of exploration. —

As well known, the Trichoptera pass through a metamorphosis. As larvæ they feed upon plant material and in accordance herewith have powerful mandibles for the purpose of biting pieces out of the stalks and leaves of the water plants; in the chrysalis stage they take no food at all; the pupa stage is passed in the well known caddice-fly houses. Before pupation the houses are closed by chitinous membranes, furnished with holes through which a water current passes. These holes must always be clean for the sake of this current. When the pupa stage is over the pupæ are forced to remove these chitinous membranes. For these two functions the animals may use an organ which may partly be able to clean the holes partly to cut those threads that connect the membranes with the sides of the house. In accordance herewith we now see that the mandibles in the pupæ are altered into a pair of scissors; the pupæ get no food, and the sole purposes of the

mandibles are to clean the holes and remove the membranes. See also THIENEMANN (1905 p. 56). Now, when the caddicelly has completed its metamorphosis, as a fully developed insect it only takes fluid nourishment, mainly honey from the flowers or fluids from trees, dew etc. — The mandibles are now useless and in accordance herewith we see that they are reduced to very small knobs. —

Simultaneously herewith the second pair of mouth parts are altered into a large licking organ (Fig. 14). —

Here we see the very same organ in the very same insect altered in accordance with the different use which the animal in three different stages of life is to make of it; from a triturating pair of pincers to a pair of scissors, and lastly so to speak to nothing, the material for the mandibles perhaps being used for the development of the labium as licking organ.

Just the same animals show another example of the same sort. When the pupa of the Trichoptera has cut the membrane, it must pass through the water, arrive at the surface, and throwing of its pupa-skin there, metamorphose into the flying stage. The passage through the water masses which are rarely more than $\frac{1}{2}$ —1 m. high does not normally last more than a few minutes, commonly only some few seconds. Some of these pupæ use an air bladder as vehicle by means of which they rise vertically to the surface. Some of them have no air bladder, and they are therefore forced to traverse the water column by swimming. —

As mentioned above, the passage takes only a few minutes, nevertheless for these few minutes in the life of the pupa the animal has developed a swimming apparatus (Fig. 15), acting in the life of the individual only during these few minutes. It consists in long black hairs on the second pair of legs, hairs to which we find no parallels elsewhere; in water-insects the swimming hairs are commonly found upon the third pair of legs. We cannot with certainty state the relationship of the Trichoptera to other groups of insects; but there is no doubt that they have secondarily accustomed themselves to pass the developmental stages in freshwater. During this ac-

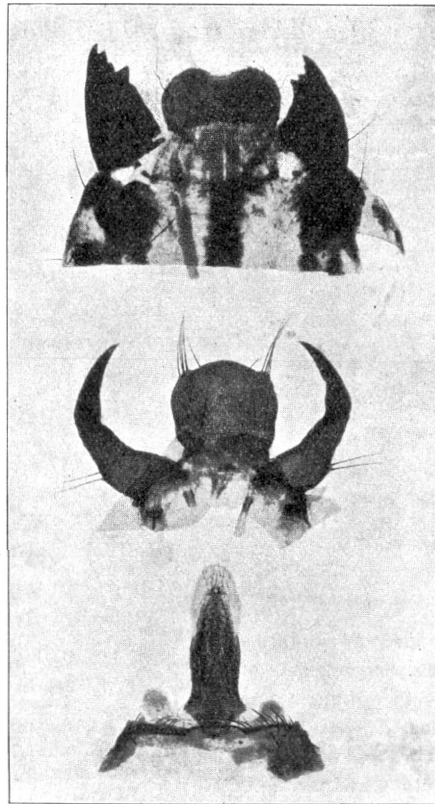


Fig. 14. Mandibles and Labrum of *Phryganea grandis*; in the larva stage the mandibles are biting organs for the purpose of biting pieces out of stalks, leaves etc.; in the pupa stage they are transformed into cleaning and cutting organs; in the imago stages they are reduced to the two knobs on the side of the labrum. The examples show that the species is able to transform its organs in accordance with use.

commodation the various demands with regard to variation in the structure of the mouth parts and special swimming organs have been made upon the organisms, and these demands they have had to comply with. In these and in many other examples taken from the life history and metamorphosis of the insects it will as far as I can see be very difficult to get any explanation much deeper than that given by NÄGELI; on the other hand we shall not deny that it is superficial. —

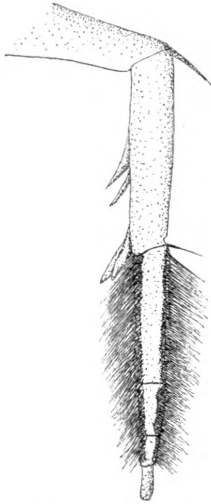


Fig. 15. *Phryganea grandis*. Second pair of legs of the pupa; the tarsus coated with swimming hairs changing the leg into a swimming organ normally used only for a few minutes in the life of the animal which normally lasts about 10 months.

The last links in the form series have commonly been regarded as very aberrant types often placed in special systematic divisions, and often in sharp contrast to the other species; they were often regarded as very old forms (viz. *Leptodora*). Later on when we got to know the intermediate stages and our comprehension of the anatomy and biology of the forms was augmented it was evident that they were only to be regarded as final links in long developmental series of species and genera, belonging to groups whose habitat was originally another and to which they were primarily adapted. Accumulating from species to species from genus to genus, the variations firstly in instincts and later on morphologically in specific characters have mounted up; simultaneously with this the species slowly withdrew from the life conditions and the habitat which may be regarded as those to which the group was originally adapted.

In the new surroundings the most aberrant forms from very different parts of the animal kingdom meet each other. The new life conditions impress a common stamp upon these systematically very different forms (Plancton characters, cavern characters etc.). Because of the quite different organisation of the different groups from which the units originate, the demands made by the new habitat are complied with in quite different ways. An example will show this. In the surf region of our larger lakes as well as in our rivers the larvæ of Trichoptera and the larvæ of Odonata meet each other; no connoisseur (Fig. 16—19) of these groups will place their native home here. The first of these two groups has the building instinct, the other not. The body of the Phryganids as well as their well known caddice houses are originally cylindrical and so is the body of the larvæ of the dragon flies. In the surf region of our lakes some of the Trichoptera larvæ, in order that they may not be swept away by waves, flatten their houses either by means of large flattened stones or by means of grains of sand; with these grains they construct winglike expansions on the sides of the cylindrical tube, in this way altering their house from a cylindrical to a discoidal one, their body itself remaining cylindrical as is the case in the whole group. On the other hand the larvæ of the dragon flies have no building instincts and no spinning power. If they are not to be swept away by

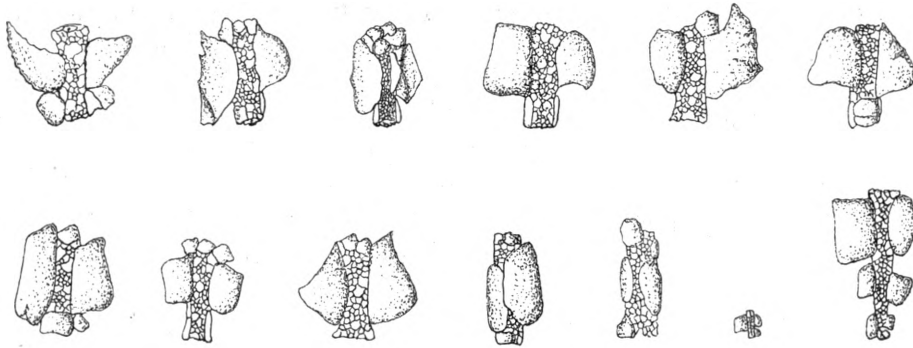


Fig. 16.



Fig. 17.

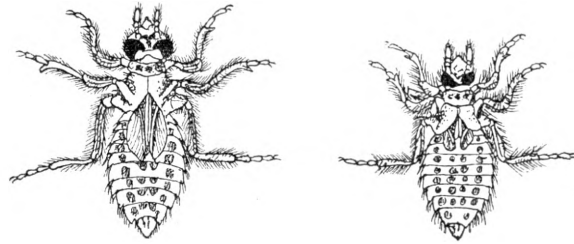


Fig. 18.

Fig. 16—19. Insects from the surf region of the Furesø.

Fig. 16—17. Organisms with spinning power (*Trichoptera*: Fig. 16. Larvahouses of *Goëra pilosa*, Fig. 17 of *Molanna angustata*) flatten their houses normally cylindrical, by means of large stones on the side of the house (Fig. 16) or by means of sandcorns glued to each other (Fig. 17).

Fig. 18—19. Organisms without spinning power *Odonata* (*Gomphus vulgatissimus*). (Ephemeriidæ (*Heptogenia sulphurea*) flatten themselves).

the waves, they have only one thing to do, so to speak to flatten themselves, and this is just what they do. The body of the larvæ of the dragon flies from the surf region of the lakes and from the rivers is very much flattened, almost as flat as the body of lice; the abdomen is flattened and so are the femora and tibia; these larvæ differ very much from the cylindrical ones from our ponds and ditches. Quite the same is the case with many of the larvæ of Ephemeriidæ, belonging to the same localities, especially the mountain rivers and rivulets; all these larvæ have likewise no spinning power (STEINMANN 1907, WESENBERG-LUND 1908 a).

That all these different form series and developmental lines should originate

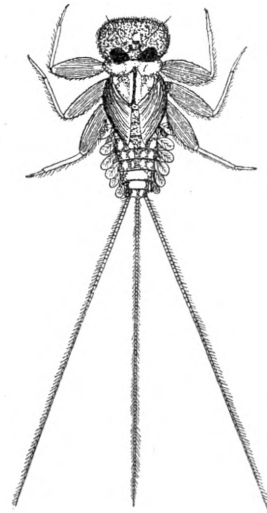


Fig. 19.

discontinually from variations tending in no definite direction, seems to me quite impossible to suppose. With regard to all form series there seems to be a conspiracy of silence on the part of the adherents of the mutation theory. Especially because I know that extensive papers relating to the form series and "Rassenkreise" are under preparation, I will here not enter upon the subject in detail.

Before entering the question with regard to the systematic value of the units in the formseries it may just be mentioned that the form series of Cladocera are by no means the only ones that have been connected with the Ice Age and the amelioration of the climate.

The decreasing salinity of the sea combined with the elevation of the continents and the transformation of sounds and bays into lakes has, according to EKMAN, produced phenomena in the *Limnocalanus* species very similar to those which have been treated in this work, viz. the splitting up of *Limnocalanus* into a form series with "petits espèces" tending in definite directions. The variations in climate during and after the Ice Age have also influenced the form of the valves of *Mya truncata* and *M. arenaria* (A. S. JENSEN 1900 p. 133). Regular variations in temperature, in the humidity of the air, and correspondingly in the vegetation have produced the well-known form series of species and varieties which are snow white the whole year round in the far North, succeeded by forms which change colour during the year from white to brown or grey, and ending with forms which the whole year round are brown or grey. The best known example is perhaps the form series of ptarmigans. But a good many organisms of the palæarctic region may be regarded from the same point of view. Almost everywhere in the animal kingdom it may be supposed that the Ice Age has caused a splitting up of the species and a variation in the geographical distribution of the species combined herewith.

Every scientist working with the palæarctic animal and plant world is forced, from whatever point of view it is treated, and from a hereditary one more than any other, never to leave out of consideration that this Flora and Fauna have, geologically speaking, quite recently been subjected to one of the greatest climatic variations. In the life and the structure of the animals, in the passage of birds, in the temperature for the ripening of the sexual products the Ice Age has set its mark quite as conspicuously as the glacial striæ on the rocks, the stone masses in the moraines etc. —

It seems to be the common view that the single units in the form series are genotypically marked. With regard to *Limnocalanus* EKMAN comes to the following, presumably well founded view.

Of the two species of *Limnocalanus* occurring in European fresh waters *L. Grimaldii* (de Guerne) lived in the postglacial time in the Polar Sea and still lives in the Baltic. During the land elevation after the Ice Age *L. Grimaldii* survived in the lakes; these surviving populations were more or less altered into the typical *L. macrurus* G. O. S. It deviates from the typical *L. Grimaldii* especially by the strongly vaulted dorsal contour of the head. Between the individual fresh water populations great differences occur; an investigation based upon a sufficiently large

material will show an almost perfect transitional series between the extreme *L. grimaldii* and the extreme *L. macrurus*. The transformation is not in the first place due to the decline in salinity after the isolation: for it is more pronounced the longer the life in fresh water has lasted. In the oldest of these lakes lives the extreme *L. macrurus*, in the youngest ones, the extreme *L. Grimaldii* and both categories of lakes are typical fresh waters. From geological investigations we know that the development of *L. Grimaldii* may have taken about 6000 years; further, as every year there is produced only one single generation, there must have been about 6000 generations.

The question now arises: are the transformations hereditarily fixed or have we only to do with different qualities of the same species. EKMAN supposes that the variations in the forms of the head are due to variations in the chemical composition of the water, to the transition from sea water to fresh water. Now when it can further be shown that the form of the head varies from lake to lake and that in spite of that all the lakes are pronounced fresh water lakes, furthermore that the variations are directly proportional with the age of the lakes, then this in other words means that the reaction-norm really is different; the transformations are hereditarily fixed, and the types of the different populations are not phenotypes but genotypes (pag. 44). If the different forms of the head were only an expression of the manner of reaction of the species, the time life in fresh water had lasted would have been of no importance, and the reaction would have asserted itself immediately, at all events in the next generation.

Furthermore, if the period the species has lived in fresh water is of significance for the transformation, this cannot be due to selection of genotypes already produced in the sea or to selection among genotypes originating in fresh water. EKMAN maintains that we have to do with a hereditary restamping of the species produced through accumulation. A variation in outer conditions has through very many generations produced a variation in genotypic stamp; the variations increased in the course of time (number of generations) but without any increase of the variation in outer conditions. Only in this way are we able to understand that the most advanced types are to be found in the oldest lakes.

EKMAN is of opinion that comparatively slight variations in outer conditions may produce hereditary shifting and that a middling variation in the milieu acting upon numerous generations will produce the same effect as an extreme variation only acting one single time. We find similar ideas in works by TOWER, SEMON, STANDFUSS, HAECKER, WOLTERECK, PLATE a. o. The two species *L. macrurus* and *Grimaldii* are composed of a series of hereditarily fixed races. The *macrurus* populations are not directly akin to each other; they have originated independently of each other and are only related to the *Grimaldii*-forms.

With regard to the Daphnids of "Obere und untere Lunzersee" WOLTERECK (1908 a) has arrived at a very similar result as EKMAN with regard to the *Limnocalanus*-species (»Elementararten, fixirte Standortsvarietäten). —

According to these authors, and as far as I know others, the different races in the form series are regarded as isolated units, deriving from genotypical reaction of the species population to different habitats. If we regard them as species it is as TURESSON (1922 p. 342) quite correctly says "largely to strip the ordinary species as found in nature of one of its most characteristic qualities viz. the ability to respond genotypically to a wide range of different habitats with such units or habitat types representing various combinations of Mendelian factors". According to PLATE (1913 a p. 456) the units in the *Cerion* form series may be regarded as "Amphimutationen" (PLATE), "Kombinationsmutationen welche durch die wechselnde Kombination einer Anzahl von Faktorenpaaren entstanden sind"; later on geographically arranged by selection. The banded varieties of *Helix hortensis* (LANG) are, as well known, regarded from the same point of view. "Man kann es als sicher bezeichnen, dass dieser ganze Polymorphismus auf nichts beruht als auf die mannigfachen Recombination einer nicht einmal allzugroszen Zahl von Mendelfactoren" (GOLDSCHMIDT 1923 p. 356). Especially by the Botanists it has been maintained that Mendelism has shown that also species follow the same laws as varieties, and that the Linnean species of the present represent genetically complicated products of recombined Mendelian factors, or genotype compounds (TURESSON).

It is not without hesitation that I, who from my studies of quite another kind, namely those on the life of animals in Nature, have slowly worked my way into the results of the modern hereditary studies, venture to advance the following suppositions, which will unquestionably seem extremely heretical to most of the "exact" investigators of heredity. Nevertheless when I now venture to state some of these views, it is because all those who study the life of the animals in Nature cannot get away from the opinion, that the modern exact hereditary philosophers, deceived by the really admirable results of their studies in laboratories, have with by far too much self-confidence supposed that they could transfer the results from the laboratories and the experimental fields to Nature. Especially after having read the fifteenth lecture of BAUR (1919 p. 309) "Die Wirkung der verschiedenen Kategorien der Variation auf die Beschaffenheit einer gegebenen Population", I decided on publication. I hope I shall be forgiven the following remarks. It was with great satisfaction that, after this chapter was written, I saw that other biologists viz. HARRY KYLE (1926) from his area of exploration: the biology of fishes, has arrived at results of a quite similar nature. —

The Mendelian laws are based upon the fact that the F_1 generation derives from a crossing between two individuals, i. e. that the parental generation P only consists of two, and that all individuals belonging to the F_1 generation are full sisters. The F_2 generation is produced either as a result of crossing between the F_1 generation viz. between full sisters ¹⁾ or from crossing back to the F_1 genera-

¹⁾ or by selffertilisation of a single F_1 individual, a phenomenon which we only very rarely met with in the animal kingdom.

tion viz. between parents and children. As far as I know this is precisely one of the points where scientists, on transferring the studies in the laboratories to Nature, have not sufficiently reckoned with two facts. We will here only deal with the animal kingdom.

I. In Nature the P generation consists of one mother but very often of more than one father, often as many fathers as the mother has produced eggs. The F_1 generation in some of our largest communities therefore consists regularly only of half brothers and half sisters.

II. In Nature the F_1 generation will hardly ever be held together till maturity, and an F_2 generation will never be a result of a crossing between full sisters. —

These facts are most conspicuous in the case of the marine communities.

ad I. It is a well known fact that the majority of all marine animals: *Spongia*, almost all *Coelenterata*, *Echinodermata*, *Polychaeta*, *Nemertea*, *Brachiopoda*, *Bryozoa*, *Enteropneusta*, *Tunicata*, *Placophora*, the primitive *Prosobranchia*, most of the *Lamelli-branchiata* and by far the greater part of all the *Pisces* evacuate the sexual products in the surrounding medium, commonly as clouds directly in the water.

Secondarily, in the above-named divisions the eggs may remain in the mother animals, but the sperma is carried with the water currents into the eggs. Only in a few cases do we know that a number of males and females unite in pairing balls and only very rarely do we find examples of a pairing between two single individuals. —

What is the fate of these eggs which a mother animal sends out as a cloud in the sea water? Unquestionably all those which attain fecundation from its own species will be fecundated, by no means by sperm from a single male, but from as many males as there are fertilized eggs. The eggs and the sperma are seized by the waves and intermingled between each other. Of course the possibility exists that some eggs from the same mother may be fertilized by sperms from the same father, but every one must admit that this is the exception, and that fertilisation by as many fathers as there are eggs is the rule. But that means in other words, that in one of the largest animal societies the rule is that the parental generation consists of one single mother but as many fathers as there are eggs; not as a parental generation in the laboratory of one mother and one father. It may furthermore be added that as great parts of this society die out immediately after the evacuation of the sexual products, a crossing back to the parental generation will in that case only rarely be possible.

It must be remembered that here it is a question of many many thousands of species, a very large fraction of the whole animal kingdom.

Only in the case of the *Crustacea*, the *Cephalopoda*, *Selachia*, perhaps a few *Cyprinodonts*, most of the *Prosobranchiata* and some few exceptions in all the other formerly named large groups, is there a possibility that the P generation may consist of only two individuals, but we shall see that also from this rule there are exceptions. Perhaps the future will show that there are so many that the exceptions will be the rule and the rule the exception.

It will be understood that the sexual products liberated in the sea water will be subject to a fate of the most different kind; enormous masses will be destroyed without reaching their destination; very many will meet with sexual products belonging to other species, genera or families. Even if swarmbuilding during the period of propagation will counteract the promiscuity between the single members, more pronounced here than in any other community, even if evacuation of the eggs of a female in a given locality causes evacuation of the eggs of many females, and the evacuation of sperm of a single male causes a sudden explosion of sperm from very many males simultaneously (milky coloured sea water), there is no doubt that nowhere has a F_1 generation such abundant possibilities of variation owing to the mixing of the sexual products of the same species and furthermore among units of higher order. Nevertheless if we are to place any confidence in our present knowledge, the question if variation is more pronounced in the marine community than elsewhere, as far as I can see, may most probably sooner be answered in the negative than in the affirmative. If this is really right, is it then not allowable to suppose, that this may partly be connected with the fact that the Mendelian laws are here of extremely little importance? As far as I can see, some fundamental differences in the great lines in the development, variation and conservation of the ocean fauna, compared with that of the continents, find here their explanation. I hope elsewhere to return to this point.

The fresh water fauna behaves mainly in another way. Part of the fresh water fauna: the few *Sponges*, and *Coelenterata*, the *Lamellibranchiata* and most of the *Pisces* commit the fecundation of the egg to the surrounding medium. The eggs may really often remain in the mother animal, but the sperma is evacuated directly in the water and, by means of currents often produced by the animal, brought into contact with the eggs. The eggs of the fresh water fishes are almost always deposited in the littoral region, where especially many of the *Cyprinidæ* are gathered in large shoals during the spawning period, and where the water may become milky with the enormous amount of evacuated sperma. See also DOFLEIN (1914 p. 473). With regard to *Esox lucius* I have often observed that the spawning female has been accompanied by two males, one at each side and both evacuating sperma over the eggs. The spawning trout and other *Salmonidæ* have behind them often five or six males which enter the hollow in the sand where the female has thrown its eggs and fertilise them. See also KYLE (The Biology of Fishes 1926 p. 292).

With regard to the *Anura* the total amount of eggs of a female from a single egg-laying period is commonly fertilised by a single male but in cases when the egg-laying period covers several weeks, e. g. *R. esculenta*, and where the eggs are evacuated in small portions, a single female uses a whole series of males during the spawning period and always that which is nearest at hand (BEDRIAGA 1895 p. 55; WESENBERG-LUND 1922 p. 211). In the fresh water organisms a regular pairing takes places to a much greater extent than in the sea. This is the case with all the *Crustacea*, *Snails*, *Oligochæta*, *Hirudinea*, *Rotifera*, *Hydrachnida* and all *Fresh Water Insects*. —

The last-named mode of transfer of the sperm to the eggs is the rule for the whole land fauna. If, however, we study the pairing processes in Nature a little more closely and further the literature, it may be shown that in reality in a rather formidably great number of cases and in almost all parts of the animal kingdom the fecundation of a single lot of eggs is carried on not by a single male but by two or a whole series. This assertion is based partly upon fairly numerous observations, partly upon conclusions relying on anatomical facts.

In the mantle cavity of *Argonauta* and *Tremoctopus* are found up to four male arms which seem almost with certainty to prove that the female has paired with more than one single male (See e. g. MÜLLER 1853 p. 27).

In many members of the large family *Calanidæ* we find on the first abdominal segment of the female bunches of spermatophores, often 10—15, some of them are empty, some filled with spermatozoa. Although we lack exact explorations the probability is, that all these spermatophores are by no means produced by a single male but by many, and that at all events different egg batches are fertilised from different spermatophores; we are not allowed to conclude that a single egg batch always is fertilised only by one spermatophore. —

With regard to the *Cyclops*-species we find quite the same. Very often we see a female carrying two males swimming along with them both. In this connection we may perhaps also call attention to those organisms, where stationary parasitic pygmy males occur in numbers around the genital opening of the females. Even if we lack all observations, it may be regarded as quite possible that also here a single eggset of the female is fertilised by more than one single male.

If we keep *Daphnids* in the sexual period in a jar and observe the copulatory processes, it will be seen that a female pairs with a series of males, one after the other. It is also observed, as already v. SCHARFFENBERG (1910 p. 17) has seen and correctly figured, that a female pairs simultaneously with two males (Fig. 20).

In the case of the *Rotifera* we find quite the same relations. The males of the *Rotifera* at the very moment of their birth are ready to pair with the females; they dart upon them and as the pairing process is not performed through a special opening in the body of the female, but everywhere where the penis can penetrate the body wall of the female, we also here find the peculiar phenomenon that a female is simultaneously paired with more than one male. Already KRÄTSCHMAR (1908 p. 10) has correctly observed and figured this phenomenon (Fig. 21); with

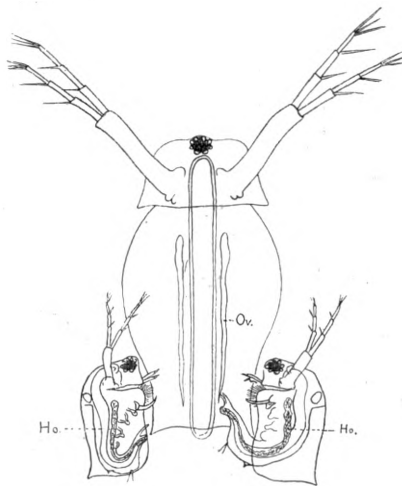


Fig. 20. *Daphnia magna* paired simultaneously by two males (v. Scharffenberg).

regard to *Asplanchna* and *Pompholyx* I have observed quite the same phenomenon. —

In this connection it may be mentioned that among Rhabdocoela, Triclada and Polyclada we find forms whose penis during the sexual act is introduced not through the genital opening of the female, but everywhere through the skin of the female and evacuate the sperm everywhere in the parenchym where the sperm is then found in balls. Herefrom the sperma wanders directly to the female genital apparatus where then the eggs are fertilized (See f. i. LUTHER 1905 p. 36 a. o.) It is obvious that also in this case fertilisation simultaneously by more than one male may be possible.

With regard to Aranea DOFLEIN (1914 p. 471) writes: "Die grosse Zahl der Männchen im Verhältnis zu den Weibchen lässt wahrscheinlich erscheinen, dass die Mehrzahl der Weibchen mehrere Mal begattet wird; Es ist solche wiederholte Begattungen durch verschiedene Männchen jedenfalls öfters gesehen worden." — GERHARDT (1911 p. 663) has observed that our common *Epeira diademata* was paired with different males. VINSON after Hesse-Doflein (1914 p. 412) has observed that the dwarf males of *Nephila nigra*, Réunion, live in the number of two upon the large body of the females and now and then pair with the female. As regards one of the bird spiders (*Dugesia hentzi*) (Gir) PETRUNKEWITSCH (1911 p. 372) has observed that one female was paired 13 times with four different males, in the morning with one male and in the afternoon with another.

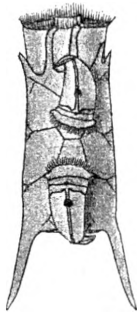


Fig. 21. *Anurea aculeata* paired simultaneously by two males (Krätschmar).

When GERHARDT (1913 p. 437) in *Liogryllus campestris* in captivity observes 76 pairings during the time $^{11}/_6$ — $^{26}/_7$ it is allowable to suppose that in Nature there is great probability that all these pairing processes are not always effectuated with one single male.

With regard to *Locustidæ* see GERHARDT p. 510.

With regard to the Formicidæ ESCHERICH writes as follows (1906 p. 58): "FOREL beobachtete bei *Myrmica* dass ein Weibchen in weniger als drei Minuten dreimal befruchtet wurde und erst ein viertes Männchen wurde abgewiesen". p. 57 he writes: "Nicht nur ein sondern zwei oder drei Männchen trägt das Weibchen mitunter auf seinem Rücken wie von FOREL bei *Lasius flavus* beobachtet wurde. Die Plätze auf den Weibchen können auch mehrfach gewechselt d. h. von verschiedenen Männchen nach einander eingenommen werden." —

More than once I have been standing near the nests e. g. of *Lasius niger*, of *L. flavus* a. o. just at the moment when the males and females swarmed out of the nests; I have then seen numerous balls of one female and three to four males; in cases like this, it is quite impossible to suppose that the spermatheca are filled only by one single male.

With regard to *Dytiscus* it has been observed that the same female has been paired with several males; this may be unnatural, but also BLUNCK in KORSHELT

(1924 p. 290) maintains that a female during the winter half of the year has at all events two copula, the egg-laying process not taking place before spring. That they should pair with the same male in autumn and spring is almost impossible; similar conditions we find among *Melolontha* (BOAS 1892 p. 247). Even if we have more than one egg-laying period we do not know if the spermatheca is totally emptied of the sperm of the first male before it is filled by the second.

HENNEGUY (1904 p. 262) mentions as follows: "Mais chez certains espèces la même femelle peut s'accoupler plusieurs fois avec des mâles différent dans un court espace de temps (*Panorpes*, *Cantarides*)".

Of the Genus *Donacia* there exists a species *D. micans* Pz. characterised by the fact that it appears in almost all the colours of the rainbow; if from a single locality, at all events here in the northern parts of Seeland, we gather about 100 specimens it is possible to arrange a series, beginning with deep red and passing through red, orange, yellow, green, and blue into deep violet, almost black. As imago the animal mainly lives upon the blossoms of *Iris*, *Cyperus* and other water plants. Here the pairing takes place, and we may often find four or five pairs pairing upon the same flower. It is a peculiar sight to see a violet male upon the dorsum of a yellow female or a yellow male upon the dorsum of a green female or vice versa. If now a hundred specimens are taken in a cage, and the beetles are marked and placed in bright sunshine it is easy to observe, how the males change their place. At one hour a blue male is sitting on a yellow female, but not half an hour later the same female carries a red male. The males jump up and down, often we have to do with pairing balls of three to four individuals. Now and then introitus penis is observed, but not always. In Nature we see the males flying from flower to flower; that in this case the spermatheca of the female should be filled by a single male is highly improbable. —

In all these cases, where I observe the rather slow females sitting on flowers (*Cetonia*, *Silpha quadrimaculata*, *Pyrrhocroa*, many *Cerambycidae* a. o.) and the males flying from flower to flower, I feel convinced that the female by no means gets her spermatheca filled by a single male, but on the contrary by many, and that the sperma from several males is to be found simultaneously in the spermatheca.

When the phenomenon is only observable in *Donacia micans* Pz. it is only because it can be so easily observed owing to the variation in colour. Most probably *Byctiscus betulae* L., showing quite the same colour variation as *D. micans*, will present quite the same relations. —

With regard to the *Libellulidae* there is no doubt that fertilisation of the same eggset by means of a series of males is the rule. I have often seen *Libellula quadrimaculata* and *L. depressa* depositing their eggs over the surface of the ponds. They are almost always followed by three or four males; now and then a copulation takes place and the egg-laying process is then continued. This is by no means restricted to one single day, but lasts many days; it is quite inconceivable that the female should always use the same male. —

With regard to *Mantis* FABRE (1923 p. 55) writes that in the course of three weeks he has seen a female being paired with seven males one after the other. —

All in all I do not think that the old dictum of LACORDAIRE (1838): “Les insectes femelles ne s'accouplent jamais qu'une seule fois dans le cours de la vie, quelque soit la durée de celle-ci” has unlimited validity. —

In all these examples, and in many besides them, it will be understood that the receptaculum seminis of the females is or may be filled with spermatozoa not from a single male but from two or several. The content of the receptaculum is a mixture deriving from several males. This means in other words that in Nature we may always reckon with the possibility that the eggs in a single lot of the female are fertilised by different males or that also in these cases the F₁ generation can never be full sisters, but only half sisters and half brothers.

Among the birds we know that at all events the *Cuculidæ* live in a sort of polyandry. BREHM (1923 V. 7 p. 437) says: “Das Weibchen schweift . . . regellos durch verschiedene Gebiete der Männchen, bindet sich an kein von diesen, giebt sich an kein von diesen, giebt sich vielmehr allen hin, die ihm genehm sind, lässt sich nicht suchen”. BREHM remarks that a female visited at all events five reviers of five different males. According to HESSE-DOFLEIN (1914 p. 473) also the *Tinamus* may live in polyandry. —

With regard to the mammalia it must be remembered that breeders of dogs and cats calculate with the possibility that in the same brood the young ones may have different fathers, deriving from pairing with different males. I for my part have in October seen a grey tabby cat pairing at eight o'clock with a yellow tom-cat, at twelve o'clock with a white and black spotted and at four o'clock with a grey. The same tabby cat was in February paired with the same yellow tom-cat as in February at twelve with the white and at four o'clock with a black one. As we know (BUMM 1923 a. o.)¹⁾ that the sperma may live for weeks in the tubes, it is also in these cases evident that the young ones may have different fathers and that the F₁ generation also in this case cannot with certainty be said to be full sisters. The above-named breeders are quite aware of this fact and cite examples where broods of twelve puppies have had three fathers and in their colour and in their coat clearly show their different extraction. With the above-named cats that was also the case. In the first case the female got five young ones; one grey, two yellow and two white and black spotted. In the last case there were six young, two totally black, two yellow, one grey and one greyish white spotted with yellow tint. —

With regard to man it must be remembered that sperma may live for a long time in the uterus. BUMM (1922 p. 21) says: “Die Fäden bleiben in den Sekreten des Uterus und der Tuben noch viel länger lebend. DÜHRSEN fand in der Tube drei Wochen nach der Kohabition noch bewegliche Samenfäden.” BUMM (p. 41) says that according to BINCH HIRSCHFELD sperma was found in the tube; mors

¹⁾ For literature relating to these questions I am in great debt to Prof. Dr. G. SAND.

occurred 14—16 hours after cohabitation. The sperm moves 2—3 mm. a minute and uses about 1—2 hours to reach from Orif. ex. uter. to the infundibulum; the eggs go much slower. According to BISHOP the time the egg uses to pass through the tube is indicated to 8—12 days. It will be understood, that also in the case of man there is the possibility with regard to twins, that the two children may have two fathers: fecundation of two or more eggs deriving from the same period of menstruation (*Superfoecundatio*) and from cohabitation with more than one man shortly after each other. —

HARBITZ (1918 p. 436) mentions the well known example that a white woman after cohabitation with a negro and a white can get a white child and a negro. Of course it cannot be denied that the negro might be father of them both, on the other hand every other explanation than that the children have had two fathers seems to be unnecessarily artificial and very far fetched. —

Whether the above named examples deriving from dogs and cats all belong to the same category *Superfoecundatio* or perhaps to the category *Superfoetatio* i. e. fertilisation of eggs deriving from different periods of menstruation and pairing with different males, cannot be decided.

The question now arises if all these examples, deriving from the animal kingdom must be regarded as exceptions or, if not as rules, at all events as often occurring phenomena. The question cannot be solved. I for my own part suppose that the phenomena are much more common than we are inclined to suppose. Human morals have prevented us from becoming aware of the real facts. It is a well known fact of which it is by no means necessary to give examples that in many cases the males pair with a number of females, and for all those cases where the testes during the rut produce sperma over a long period and the eggs from a single breeding season are not ripened simultaneously but over longer periods, weeks or months, this may be the rule. On the other hand the condition for that the female in one single sexual period shall not pair with more than one male only depends upon the force and power of the male not to loose his hold upon his harem. To get exact observations of these phenomena in Nature is very difficult and observations of animals living in captivity are in my opinion almost worthless with regard to these questions, for the higher animals almost as worthless as if we were to study normal sexual life upon convicts for life. —

Two objections may be raised to my supposition that the above named phenomena play a much greater role in Nature than hitherto supposed. It will be pointed out as a well known fact that the male among a good deal of animals after the pairing fills the vagina of the female with a secretion making the so-called vaginal plugs (*Dytiscus*, *Parnassius*, *Nematoda*, *Rodents*, *Chiroptera*, *Cambarus*). They have been regarded as means by which pairing with other males should be prevented. This supposition is not very probable, partly because they mainly occur where sperma are to live for months before use in the genital system of the female, and the

fecundation does not take place before a period of hibernation, partly because it has been observed as well by others as myself that other males try to and also do pick out the plugs by means of the mandibles and then pair with the females. —

More serious seems the objection that the female after the copulation refuses other males. I am not quite sure that this objection is more than a superstition, based upon insufficient observations. It may be doubtful, if it is stated for the invertebrates, and among the fishes the best known examples of any thing of that kind are probably found among species where it is the males which refuse the entrance of other males into their nests and not the females which refuse the males.

With regard to the mammals it must be remembered that rejection of other males on the part of the female, at all events in very many cases, does not begin before fecundation, not until after the female has been impregnated. Phenomena of refusal during the sexual period can only be effective in animals which live in pronounced monogamy, especially perhaps the beasts of prey and the birds of prey.

The question is now: Have the Mendelian laws the same validity in the case where the F_1 generation consists of half brothers and half sisters and not of full brothers and sisters or, in other words, whether the male germ plasma is homogeneous as is that of the female, viz. deriving from one single individual, or in the widest possible sense heterogeneous viz. from many individuals. Being no expert on heredity I beg others to solve this question; as far as I can see before this has been done exactly, all attempts to transfer the Mendelian laws to populations in Nature must be regarded as mere phantasies. —

But this will be more obvious if we now take into consideration the other factor alluded to on p. 211.

ad II. With regard to the F_1 generation in laboratories and in Nature there is the great difference that in laboratories the F_1 generation is kept together till maturity is reached, in Nature it is spread as soon and over as large areas as possible. Wherever there is a risk of the F_1 generation reaching maturity in the birthplace, Nature seems to prevent it. Actively and passively the members of an F_1 generation are spread; the radius of their wanderings may be short or long. It is of course absurd to suppose that they should meet again where they were born and here pair with each other; the result would be interbreeding, and in Nature this is as a rule prevented. We will here only pay attention to a few very suggestive examples. Sedentary animals almost always possess freeswimming larval stages. In the state building insects the foundation of the colony is commonly only entrusted to a single individual, the mother animal; the young ones, the F_1 generation, are neuter. In colonies which are extremely sedentary, e. g. *Aphidæ*, well known precautions are often taken to prevent the total amount of young ones from passing through all developmental stages upon the same plant individual.

Nevertheless we really find animals whose radius of action during life is so restricted that generation after generation are found to live year after year upon

the same spot or in an area which at all events is extremely restricted, organisms whose active locomotory power is very small, and which do not possess any means of spreading over other areas. We find such organisms among the fauna of the trees, in the tropics no doubt more than in the temperate zone; to these belong especially tree snails; further some organisms of the freshwater fauna, especially that in very small ponds, perhaps the fauna in very secluded alpine valleys and on alpine tops, insular life, rats restricted to special ships, special quarters of towns etc. In these cases but they are all exceptions and not the rule, race-formation combined with wanderings and isolation may go on in accordance with the Mendelian laws.

Most probably it is from these very exceptions that the Mendelists have got most of their well known examples.

Now, as far as I can see, with regard to the free populations of Nature we are forced to reckon with the following facts. It cannot be denied that in great parts of the animal kingdom the P generation consists not of two single individuals, a father and a mother, but of many, a mother and as many fathers as there are eggs; further that in other parts of the animal kingdom the P generation in very many cases consists of one mother and a different number of fathers, e. g. among insects, where the term "chain-fertilisation" may in many cases be regarded as correct, finally that in all the cases where the P generation normally consists of only one mother and one father we are forced always to reckon with the possibility that the progeny of the same brood has more than one father, and that this may so often be the case that we do not know what is the rule and what is the exception.

It must furthermore be admitted that in the animal kingdom it is the rule that the F_1 generation in Nature is never as in the laboratories kept together till maturity; on the contrary it is spread over areas, the extension of which in many cases is enormous, and progeny is therefore almost always produced between individuals by no means related to each other.

The modern students of heredity have of course a clear understanding of the fact that a whole population deriving from a uniform F_1 generation is only very rarely to be found in Nature and that here the freest possible crossing is the rule. See e. g. BAUR (1919 p. 314) and many others. On the other hand, they are nevertheless of opinion that they, as BAUR often says "leicht" are able to calculate the hereditary results of "ganz unbeschränkter Paarung" carried on in "eine Reihe von Generationen", in populations living under quite natural conditions. I especially refer to BAUR's views with regard to crossing in populations of rabbits, very often mentioned in the literature on heredity, and undoubtedly regarded as the paradigm of a normal crossing process in populations.

Biologists will here have the greatest difficulty in following the students of heredity. From a biological point of view we may be allowed to say to the representatives of the new science, which from its first dawn has decorated itself with

the very suggestive word "exact", that all these calculations, relating to "free crossings" in the populations in Nature are quite hypothetical and from a hereditary point of view by no means better scientifically grounded than the hypotheses relating to the origin of the species which biologists, palæontologists, and embryologists set forth and which the students of heredity commonly characterise as mere phantasies.

When BAUR (1919 p. 344) writes as follows: "Für die grosse Mehrzahl aller Organismen kommen als Auslesematerial nach dem heutigen Stand unseres Wissens nur die Mutationen der Kategorie I in Betracht" viz (p. 286) "die häufigste Kategorie die darauf beruht, dass aus unbekanntem Ursachen Individuen auftreten, welche gegenüber der Ausgangsrasse einen mendelnden Grundunterschied aufweisen", I suppose that this is extremely exaggerated.

If my conception of the composition of the P generation combined with my conception of the fate of the F_1 generation in Nature is correct, I cannot see better than that the Mendelian laws, in the way they are formed, are only to a very slight degree able to assert themselves in Nature. If the students of heredity would restrict the Mendelian laws solely to the study of the combination of the gens, my criticism would be irrelevant. On the other hand if as especially BAUR a. o. seem inclined to do they also use them as a basis for the study of evolution in Nature, I cannot see better than that I have here pointed out a fact which in this case cannot be totally omitted in the calculation of the Mendelists.

Nevertheless I can imagine that now the students of heredity will maintain that all that is gained by this demonstration in reality is only of very slight importance. The numbers of "mendelnde Grundunterschiede" and their significance for selection will be the same. The only difference will be that we now are forced to suppose that a sort of selection sets in from the very moment when the egg is able to be fertilised, not only from the moment when the young one leaves the egg; furthermore that it has only significance as deepening our conception of the variation of organisms due to cross-fertilisation; our conception of the work of the selection will be unaffected. I do not think this supposition is correct. Owing to the very fact that the cross-fertilisation between the individuals of a species is of a much more complicated nature than hitherto believed, the variations will be obliterated as soon as they appear. Without a certain degree of stability selection cannot work, at all events only where it is combined with isolation, and it is just this stability which especially in the oceans in my eyes commonly does not exist. I expressly only use the word variations; in the deep cleft supposed between the terms genovariation and phænovariation I have no confidence.

As far as I can see, something in the above-named demonstration supports the supposition that hybridisation between units of higher order as an origin of species plays a much greater role than hitherto believed.

We will now return to the form series of the Daphnids and shortly recapitulate the foregoing.

As mentioned elsewhere I regard the freshwater plancton as one of the oldest communities of the earth. It may in this respect be remembered that the Ostracoda, the nearest relations of the Cladocera, go back to the oldest epochs of our earth and that the ehippia of the genus *Daphnia* as well in Sweden as in our country have been found in the deposits of arctic clay lying below the peat deposits and together with arctic plants: *Dryas octopetala* and *Salix polaris*. The ehippia cannot be distinguished from those which are formed nowadays as well in the arctics as in more southern latitudes by *D. pulex*. It may be regarded as highly probable that this species has lived in immense numbers in the ponds and in the littoral region of lakes immediately after the melting period of the ice. As pond- and littoral species *D. pulex* followed hot-foot upon the ice and was spread over vast areas of the arctic region. Everywhere, but most in the northern temperate zone, in countless localities spread over the vast areas, a tendency to a more pelagic life, to an emancipation from the bottom and littoral region, appeared. In accordance with the improvement in climatic conditions and rising temperatures *D. longispina* split up into numerous races, the most primitive of which were not to be distinguished from *D. pulex*, and the most aberrant (*forma ambigua*), very nearly related to *D. cucullata*, accustomed themselves to the new life conditions. Hybridisation between *D. pulex* and *D. longispina* still takes place to this very day. The races arrange themselves in form series beginning in the far north with forms without any seasonal variations, and ending e. g. in our lakes with races like *D. lacustris*, *D. galeata* and others, all reverting in winter to forms which are not to be distinguished from those races which under arctic conditions have hardly any seasonal variation at all.

As researches in our day have shown that all our present *D. longispina* races exhibit almost the same appearance up to abt. 14° C., we may suppose that up to the time when the temperature in the lakes had not yet continuously and over long periods reached above 14—16° C., all the different *D. longispina* colonies were rather similar in appearance. At this temperature the shorter and clumsy races, adapted to lower temperatures, are no longer able to keep floating in the warmer water with its smaller specific gravity and viscosity; other demands are then made upon the organisms. Along with the morphological variations: a longer A, a longer spina, and narrowness of the valves, go variations in propagation. The sexual periods become more and more rare; acyclic reproduction more and more pronounced. According to the principle of adaptive radiation the possibility of the appearance of different local races arranged in series of forms was given, each race being only the expression of the special way in which seasonal variation in each locality developed. The supposition is strengthened by the fact that in more southern lakes where the summer temperature mostly remains at 14—16° C., and where most probably the amount of organic matter (detritus etc.) (Alpine lakes) is smaller, local variation is but small; furthermore we here find races without, or with a very slight, seasonal variation, the specimens are on the whole short and clumsy, and their colour

is often reported to be more or less reddish and brownish; sexual reproduction still takes place in the majority of these lakes, and very many ehippia are formed. I refer the reader to the explorations on *D. longispina* in Scotland (JAMES MURRAY 1905), Iceland (W.-L. 1906), Norway (HUITFELD KAAS 1906), Achensee (BREHM 1902) and most probably also many Swiss lakes (ZSCHOKKE 1900, BURCKHARDT 1899—1900). The result is that all these forms, living perhaps hundreds of miles apart, exhibit a greater likeness than the races in our own and the south Swedish lakes which live at a distance of comparatively few miles from each other. The explanation why the different summer forms in the Baltic lakes with their high temperatures vary to such an almost incredible extent may partly be sought in the fact that they have a double origin (*abbreviata* and *intermedia*). During the immense spaces of time from those remote periods when the summer forms began to assert themselves and down to our day, all the numerous races returned, and still in our day go back, if no longer to the starting points of the form series, still to the forms nearly related to them (*obtusifrons* and *intermedia*).

Now somewhere in this form series, with augmenting length of A in the summer half of the year from North to South, the very remarkable phenomenon occurs that forms arise which, as long as the explorations of Cladocera have been carried on, have been regarded as special species, nay more than that, originally as well marked genera, *Cephaloxus* and *Hyalodaphnia*, or as they are now called: *D. longiremis*, *cristata* and *cucullata*. They all exhibit characters which may be regarded as pronounced species marks, viz. constant loss of one of the long swimming bristles, 1st pair of antennæ placed on the tip of the rostrum, not on the posterior edge of the head carapace, loss of pigment spot. The species have their maximum in the summer half of the year; they do not occur, as *D. longispina*, also in small ponds, only *D. cucullata* has been found here, but the occurrence here is unquestionably secondary. *D. longiremis* is a pronounced coldwater form, constantly living in the depths of the large lakes, the other two, especially *D. cucullata*, are pronounced warmwater species. Common to all is a pronounced tendency to acyely. *D. cucullata* begins in Sweden near the zone of the Mid-Swedish large lakes; it is very rare in Norway, absent in Scotland, but common in England, in Denmark, and in the southern part of Sweden. *D. longiremis* and *D. cristata* are almost only known from Norway, Sweden and Russia, mainly in the northern part of the temperate zone, but not from arctic lakes. (FREIDENFELT 1913 p. 242). *D. longiremis* seems, according to its life history, to be a pronounced glacial survival. The two species (*Cephaloxus*) seem to be most nearly related to *D. longispina*.

Now the very remarkable phenomenon occurs that also *D. cristata*, and especially *D. cucullata*, has a pronounced seasonal variation, and especially that this occurs in the same manner as in *D. longispina*, showing prolongation of A with rising temperature, only this prolongation is much more pronounced in *D. cucullata* than in *D. longispina*. $A + B$ is often $> V.$, in *D. longispina* it is almost always $< V.$ Simultaneously herewith, however, we also see that the modelling of the

crista goes on in the summer races in a somewhat different manner than in *D. longispina*.

The crista is never broad as in *D. longispina* var. *lacustris*; it is always pointed, but has never a pronounced well defined thornlike tip, which is often found in *D. longispina* var. *galeata*. As in *D. longispina* the apex may often lie in the prolongation of the longitudinal axis, but is often, which is never or at all events very rarely the case with the races of *D. longispina*, either curved downwards or dorsally (var. *procurva* and *retrocurva*). It will therefore be understood that even if the seasonal variation in the main point, viz. prolongation of the long axis of the body, asserts itself in the same manner in the two species, nevertheless the seasonal variations in their final results are not the same in *D. cucullata* and *D. longispina*. Owing to that fact too we are entitled to keep the two species distinct. —

The most peculiar fact, however, is as mentioned above, that also these, during summer, well separated species in all their races revert to one and the same common stamp during winter, identical with the common winter form of *D. longispina*. The result is that we can only with the greatest difficulty distinguish the winter forms of the two species from each other.

In the winter form of *D. longispina* a rostrum is very often but faintly developed; the pigment spot has not always pigment.

The winter form of *D. cucullata* is as clumsy as that of *D. longispina*. In lakes like Esrom lake where we simultaneously have *D. longispina* and *D. cucullata* the two species can only with the greatest difficulty be distinguished from each other during winter. As far as we know the same result has been gained from other European lakes. It is not until the lake of Lugano that the great conformity of the individuals disappears (STEINER 1913 p. 92). On the three South European peninsulas *D. cucullata* seems to be rather rare. (The lake of Scutary). It is recorded from Victoria Nyanza as *H. Jardinii* (DADAY 1907 p. 245). Throughout the whole of Europe the two species may be found together, often in the very same lake. This is mainly the case with the lowland lakes of the Central European plain. In Switzerland and especially in lakes under more arctic conditions *D. longispina* preponderates, or *D. cucullata* entirely disappears. Whilst *D. cucullata* is the pronounced lake form, *D. longispina* in its different races is found as well in ponds as in lakes, in the ponds often together with *D. pulex*, in the lakes together with *D. cucullata* and very rarely together with planctonic races of *D. pulex* (pelagic races with "Nebenkämme").

The question now arises: In what way are the links in this form series to be interpreted?

By Idiokinesen we understand with LENZ (1912 p. 571) the development of new hereditary predispositions ("Erbanlage") in the germplasma, produced by outer factors. With HAECKER (1921 p. 166) we may suppose that Idiokinesen may arise in three different ways.

1. The sudden appearance of hereditary variations occurring in the direct progeny of the generation which is subject to the variations in outer conditions (TOWER).
2. The variations in outer conditions may act through a series of generations before the variation in the germ plasma, slowly prepared in these generations, suddenly manifests itself as mutation. (NÄGELI, WEISMANN).
3. Variations in outer conditions acting in the same way during a long series of generations may act upon the germ plasma not suddenly but slowly through a series of very small variations which accumulate from generation to generation (SEMON, EKMAN, STANDFUSS).

In order to understand the units in the *Daphnia*-form series we may presumably use the second and third explanation. The single lake races of *D. longispina*, and *D. cucullata* (forma *galeata*, *retrocurva*, *procurva* etc.) may be explained in accordance with the third possibility, the same which EKMAN has used to explain the different biotypes of the *Limnocalanus macrurus Grimaldii* series; the appearance of *D. longiremis* and *cristata* but especially *D. cucullata* may be explained by the second possibility.

According to EKMAN the single units in his *Limnocalanus* series may be regarded as genotypically modified; they may be regarded as blastovariants (WOLTERECK). The proofs of this conception which EKMAN is of opinion he is able to give for his material I cannot give for mine. We are perhaps able with EKMAN to maintain — and with the same certainty as he for the *Limnocalanus* material — that the transformations of the Cladocera have taken place through about 6000 years; on the other hand we have, as is the case with the *Limnocalanus*, not the slightest knowledge with regard to the history of the immigration of the Daphnids. We only know, as mentioned above, that the ephippia are to be found in the clay of the inland lakes, deposited at all events immediately after the Ice Age, further that these ephippia cannot be distinguished from those from the present time. On the other hand we have not the slightest idea from where these Cladocera have arrived, nor of the number of generations produced from that time to our day (see p. 208).

EKMAN is able to maintain that the variations in salinity are the main causes of the variations in *Limnocalanus*. In a very similar manner I am able to maintain that the regular variations in the falling velocity of the fresh water organisms dependent upon those of the viscosity and specific gravity, again dependent upon the variations in temperature, are the main causes of the seasonal variations in Cladocera as well as in the other plancton organisms. On the other hand we are not, as is the case with EKMAN, able to say that the variations of the *Daphnia*-races are proportional with the age of the lakes; in my opinion Ekman's chief proof of the correctness of his views lies in that very point of regarding the units of his *Limnocalanus* series as genotypically remodelled. The peculiar phenomenon unknown in Ekman's material, that the different *Daphnia* races in winter revert to the very same form, speaks strongly against any attempt to regard these races from the same point of view.

My own conception of the *Daphnia longispina* and *D. cucullata* races is only a subjective one without any special scientific value; on the other hand it is based upon a study continued through not a few years.

Our present-day populations of the pelagic *Daphnia* species are presumably fairly form-fixed and very little influenced by variations in the outer medium. Most of the explorations seem to show that. We know that *D. longispina* and *hyalina* var. *pellucida* from 1868 to 1926, from the time when P. E. MÜLLER found it in Tjustруп- and Sorø lakes and till now, does not show the slightest difference.

This observation is not really very valuable, but in my opinion about thirty times more valuable than those laboratory explorations which from only two years experiments expect that the species may be genotypically altered by means of variations in outer conditions. The observations seem to show that as long as outer conditions are not appreciably altered so long the race is formfixed. On the other hand I feel fully convinced that if the temperature again went slowly down and we got a new Ice Age, then all the lake races would revert again to the old common one; and this view will, I feel convinced, be shared by most of all who have more thoroughly studied these animals for years. That the races if we take them into our laboratories and vary the life conditions, in the course of a few years should immediately feel obliged to obey orders is in my eyes too much to expect, and their disobedience in this respect is no proof of a break in the range of variation or of the stability of the two types.

It is quite useless and of very little scientific significance to clear up if these races are only phenotypes or really genotypically transformed. Here as everywhere I feel convinced that a more thorough study carried on in Nature, and combined with palæontological and geological dates will show that the sharp line of separation between the two terms genotype and phenotype, however much the students of the exact research of heredity will protest, is the work of man. Others have said that before me. In Nature it does not exist; Nature does not work after sharp lines. —

If the *Daphnia*-races nowadays are relatively formfixed this may be combined with the fact that also the waters of our lakes, i. e. the "outer conditions", are nowadays in their regular annual physical and chemical conditions a rather well stabilifed outer factor. From this there is however one single, really very significant exception. In the large Baltic laketerritory, just where the populations deviate most, and where they are subject to the strongest demand with regard to variations in the bearing power of the freshwater, owing to the cultural work of man, the amount of organic matter, carried out into the lakes, is augmenting year after year. The nutritional biological value of the watermasses increases year after year. Now knowing from the explorations of WOLTERECK how great a significance the amount of nourishment has with regard to the height of the crista, the thought is by no means far fetched that the ever-increasing amount of organic matter in the water

of our lakes has had and will in a still greater degree have accumulatory value with regard to the height of the cristæ of *Hyalodaphnia*, higher here than elsewhere known. Corresponding phenomena we find in the melanistic Lepidoptera in Hamburg (HASEBROEK 1914).

With regard to the distribution of the different races of *D. longispina* and *D. cucullata* I confess there is a problem which has troubled me very much, and which is more difficult to solve, than we have hitherto thought. It has often been mentioned that each lake so to speak has its own *Daphnia* race. Fearing that I had exaggerated this fact in 1898—1908, I have now again in 1924—1926 taken large plancton samples from the same lakes as then. The result was the same as in 1898—1908. In every lake I find only one race of the two species during summer, each with its special characters, and these marks are now the same as then: *D. cucullata* forma *procurva* in Juul lake, *D. longispina* f. *ambigua* in Esrom lake *D. longispina* f. *pellucida* in Sorø and Tjuststrup lake; furthermore the very high *B. coregoni* in Juul lake and Tjuststrup lake and the very low in Furesø, the same type which P. E. MÜLLER has figured in 1869.

Scientists who do not possess sufficient knowledge of the life of the Daphnids in Nature will most probably give the following explanation of this part. Most probably our lakes have been populated by ehippia, carried out into the lakes by currents of water, by birds a. o. Genetically the material has of course been extremely heterogeneous. The more the colony in a given lake went over to being acyclic, and when amphimixis did not occur, the more the result would be that the colony would be split up into a number of pure lines. It cannot be denied that it now seems as if selection, in accordance with the schemes of the students of heredity, has preserved those among the different variants which have been best fitted for the environment, and that this work in most of the lakes may now be said to be mainly finished. Later on, through thousands of years, the victorious variant, accumulatively accustomed itself to the milieu and got its definite form, unchangeable as long as the milieu was not altered, apparent genotypically fixed, but in the life of the species only to be regarded as a phenotype.

However tempting the explanation may be, in my eyes it is quite unsatisfactory. The fact is that these lakes are not isolated watermasses as those in our aquaria. At their borders and in their bays we find littoral races of *D. longispina*; in the case of small lakes which flow out into larger lakes, we find different races in every of these lakes. We are forced to take it for granted that birds and currents year after year carry ehippia from the small waters into the large ones.

How then is it possible that nevertheless the races in the large lakes present themselves as homogeneous and formfixed? I can only find two possibilities. The one is that the new immigrants are already modified in the first generation, the other is, that not being accustomed to the life in the lake, they die out. Both explanations are in my eyes quite insufficient. This point must be decided by future explorations. I propose an exploration of the different races of *D. longispina*

and *D. cucullata* in the lateral lakes with outflow into the larger lakes run through by the Gudenaas; all these lakes, the lateral lakes and the main lakes, have their own races. "Uferflucht" cannot explain this phenomenon.

As well known we have, in lakes lying only a few kilom from each other, viz. Furesø and the lake of Frederiksborg castle, races of which the one is pronouncedly acyclic, the other year after year monocyclic with a sexual period occurring in autumn. It being expected that variation would assert itself in quite a different manner in these two lakes, in the one of which amphimixis occurred regularly in the other not, the exploration was carried on. The result was that no difference in the variation could be observed, and the two races could only with difficulty be distinguished from each other. I got the idea that if variation on Mendelian lines in this case should be of significance, we were entitled to expect that during the period of its life, when the population went over from cyclic to acyclic propagation, the population would be split up into a number of biotypes, of which at last only one single one would be selected out. Of course I could not expect to find a lake in which the Daphnids were in a period of variation, caused by transformation from cyclic to acyclic propagation. On the other hand it was just these considerations which caused those, relating to the fate of a P and a F₁ generation in Nature itself. It seemed to me as if variation on Mendelian lines in Nature itself, owing to the complicated processes of cross-fertilisation mentioned pag. 219, only rarely get opportunity to assert itself morphologically. On the other hand it may have significance for biological variation (variation in reaction norm without morphological variation), but morphologically at all events mainly during the mutable periods, and then as total mutations after accumulation. These total mutations may be caused by slowly remodelling of the germ plasma, perhaps originating from hybridization between units of higher order, but according to my opinion mainly owing to abrupt environmental changes.

It is in this way we will now consider the above named well-marked species which appear in the form series, especially *D. cucullata*; these may be interpreted in another manner than the different races of *D. longispina*.

If it be correct, as always has been done, to regard them as well-marked species (see p. 222) and if they, direction-determined, occupy their place in the form series, varying in accordance with the other units, showing extreme development and accommodation to augmenting variations in outer conditions, an accommodation which had already begun among the *D. longispina* races and extends over areas where this accommodation preponderates in an ever increasing degree, simultaneously with the fact that the *D. longispina* races as lakes races retire from these areas, then there can in my opinion be no doubt how these new species are to be interpreted.

They may indeed be regarded as mutations (Idiomutations PLATE), but they

are by no means casual, in their origin independent of variations in outer conditions, without definite direction ("richtungslos"). They are prepared and determined by previous modifications. The climatic variations taking place through thousands of years have influenced the germ plasma. We have here to do with a genotypical remodelling, caused by accumulatory forces, a summing up of uniform influences from without, acting over periods of time almost inconceivable to human thought and manifesting itself suddenly and simultaneously in very many individuals of the population.

In reality the suppositions set forth here are very much akin to those set forth with regard to the climatic variations of a series of Lepidoptera *Polyommatus phlaeas*, *Arctica caia*, the *Vanessa* species a. o. I here refer the reader especially to the papers of STANDFUSS, FISCHER, SCHRÖTER a. o. We find them often in the genetic literature.

HUGO DE VRIES has especially laid stress upon the opinion that the single species, apart from the non-hereditary fluctuations over very long immutable periods, lasting for thousands of years, suddenly enter upon mutable periods, during which the species is split up into elementary species or biotypes; these periods are always short, compared with the immutable ones. The term elementary species is always very problematic and difficult to define. Nowadays a species like *D. cucullata*, which during winter can only with difficulty be distinguished from *D. longispina*, may of course be regarded as an elementary species; on the other hand it has always been regarded as a systematic unit of a higher order.

TURESSON (1922 p. 343) says: "We are thus forced to the conclusion that the present-day species represent the necessary outcome of the complex processes of selection in this epoch of the earth history (cp. HERIBERT-NILSSON 1918). As a natural consequence we are led to the inference that a change in the non-living world brings about a corresponding change in the living, inducing a recombination of Mendelian factors now distributed in organisms, and resulting in the formation of new genotype compounds or species."

TOWER (1906 p. 314) says: "I am therefore of the opinion, that the evolution of the genus *Leptinotarsa* and of animals in general, has been continuous and direct, developing new species in migrating races by direct response to the conditions of Existence." — Quite similar opinions have been set forth by DARWIN, PLATE, EKMAN, KYLE a. o.

Even GUYÉNOT (1924 p. 45) admits the existence of formseries but restricts himself to the following short remark: "Cette continuité dans le sens de l'évolution n'exclut pas cependant la notion de discontinuité évolutive. La transformation résulte ici encore d'une série de variations discontinues, plus ou moins étendue, qui n'ont de commun que le fait de se produire dans un sens défini." The question is only: How can a series of variations simultaneously make their appearance discontinually and direction determined?

One of the mutable periods for the *Daphnia* species was caused by the Ice Age and the amelioration of the climate after this period.

From the Ice Age to our day Nature has accomplished an experiment with regard to heredity with the animals of the palæarctic region, so immeasurably grand that human thought is almost unable to apprehend it: The object of the experiment was to study the influence of the altitude of the sun at the borders of the melting ice from the temperate zone to the arctic region. Like a magnet the melting ice drew animal- and plant life towards the North. The conditions of the outer medium being in all other respects almost the same, the altitude of the sun varied incessantly during the wanderings towards the North. Through a number of generations, immeasurable by human thought, the organisms altered biologically and morphologically.

We are here able to get to know Nature as the great experimenter; she and she alone determines the first condition of the experiments relating to the fixation of qualities acquired through variations in the outer medium being carried on: namely the immeasurable periods of time. The races and species tending in definite directions and varying in accordance with environmental variations in the form series are the result of influences in the outer medium acting in the same manner over immeasurable periods of time. And what then was the real result of this variation, beginning long before man appeared to inhabit these inhospitable territories? Varieties, varieties, and again varieties, and furthermore some relatively few "good" species, differing but slightly from the mother species. Never and nowhere did the organisms vary more than when they were connected with each other by innumerable, small transitional links almost undetectable to the human eye. Sudden, sharply delimited links, which have the appearance of a total mutation, are always rare and always determined in accordance with the formseries; they can only be regarded as caused suddenly and by accumulation by the exaggerated development of just those structures, the almost invisible, slowly increasing development of which just characterises the single forms and race units in the formseries. — If we look at the formseries of ptarmigans, of foxes, of hares, of certain molluscs, of lepidoptera and some beetles the result is always the same.

Now when we shortlived human beings start experimenting, we take the organisms into our laboratories; they are here exposed to variations in the outer medium, to which they never have found and never will find any parallel in Nature. We experiment with the organisms for some months, for some years. If we have been able in the laboratory, owing to special variations in outer conditions, to create a new biotype and this, being brought back to the natural ones, reverts to the old form, all writers on heredity, all our present day alchemists of the study of evolution, all those who regard the organisms merely as machines i. e. all those which have entirely lost touch with living nature, who cannot see the wood for trees, nor the laws for figures, solemnly declare that this result is a proof for their view that acquired characters are not hereditary. —

Laboratory studies may indeed lead to results which dazzle by a seemingly far greater accuracy than that which it is, as a rule, possible to attain through studies in Nature. It must, however, be kept in mind that those so-called exact

results are arrived at by methods of research which have their strength especially in their one-sidedness, but for that reason they have also hidden in them all the sources of erroneous researches. We may therefore be justified in doubting how far this accuracy in many cases is anything but an illusion, and whether the results arrived at in Nature, with due consideration for its endless and manifold qualities, have not on the whole as great a scientific value, even if the results in question appear in a more unostentatious and less dazzling form.

The modern experimenter not only demands that just those variations, produced under those variations in outer conditions, which he is able to produce, must be hereditary, he also wants to decide the time to be used by the species, and this must by no means exceed some months, at most some years. Moreover he demands that he must be present at the very moment of the birth of the new type, and so to speak play the role of midwife. If all these demands are not fulfilled, he is in the negative results of his experiments inclined to find a support for his views, that variation in the composition of the germplasma in this way is an impossibility, and as a further result that discontinuity governs evolution. If the experimenter would only remember how often, during his laboratory work, he so to speak exerts violence against just that species from which he expects new species to arrive, he would perhaps better understand that the results obtained from all his experimental work hitherto produced, as far as I know, can almost all only be enrolled in the vast category of pathological phenomena. —

In the literature relating to heredity and biology we very often find thoughts very nearly related to the above mentioned ones.

GOODRICH (1924 p. 108) says with regard to modern developments of the study of heredity and variation on Mendelian lines: "Fortuitous changes in the inherited organization, in the complex of factors transmitted, are left as the only elements of primary importance, the only stones of which the edifice is built."

MEISENHEIMER (1923 p. 79) says: "Und diese Unsicherheit haftet bis in die neueste Zeit hinein wohl so ziemlich allen Versuchen an, welche durch gleichsinnige Faktoren typisch intermediäre Zustände der zweiten Tochtergeneration vor allem auch bei Artkreuzungen erklären wollen. Vielfach ist dabei jede Spur experimenteller Exaktheit aufgehoben worden. Man weisz nicht, wie viele Faktoren es sind, welche Art sie sind, man operiert mit ihnen, mit zahlenmässigen Ergebnissen in weitgehendster Willkür bis alles stimmt und man endlich die Mendelsche Formel gesichert hat.

(p. 128) Für den in seinen dogmatischen Voraussetzungen konsequenten Vererbungstheoretiker giebt es keine Umbildung, keine Neugestaltung, keine Neuschöpfung von Genen, es kann also niemals eine neue Form, also etwa eine neue Art durch Hinzutreten eines positiven neuen Gens entstanden sein. Nun kennen wir die Mutationen. Bleibt man konsequent — dazu haben nicht mehr allzu viele den Mut — so darf die in ihnen sich äussernde positive Erscheinung einer Abänderung des Genotypus keinem positiven Neubildungsprocesz ihre Entstehung verdanken. . . . Was durch die

Kreuzungs- und Züchtungsmethode in der Vererbungslehre an wertvollstem exakten Gewinn geschaffen worden ist, es beginnt völlig erdrückt zu werden durch die fast ungeheuerliche und ständig zunehmende Last hypothetischer Speculationen, die darüber gehäuft wird. . . . Das Züchtungs und Kreuzungsexperiment greift über die Zuständigkeit seines Richteramtes hinaus, wenn es auf Grund seiner Ergebnisse so gut wie alle Vorstellungen der Evolutionstheorien glaubt als gegenstandslos abtun zu können".

It may perhaps be rather reasonable to call the attention of the reader to the following five indisputable facts.

1. From the Ice Age to our day we do not know aberrant types of animals which we may suppose have arisen during these immense species of time.

2. All that part of the Northern avifauna, which we might expect to find in the kitchen midden, bears a message from those remote times that this avifauna was the same, the same species, which we find nowadays

3. Owing to the admirable faculty of observation and great descriptive power of the Egyptians we possess an almost incredible knowledge, as far as I know, very little exhausted from a zoological point of view, of the mammals and avifauna of a country, from a period dating back more than 5000 years. I refer especially to the extensive works of LEPSIUS: *Denkmäler aus Ägypten*, Bd. 3—4; STEINDORF: *Das Grab des Ti*; P. E. NEWBERRY: *Beni Hassan I—II*; FLINDERS PETRIE: *Tell el Amarna and Medum*. It is not only the large mammalia like the hippopotamus, the baboon, and the *Oryx* antelope (viz. BENI HASSAN I Pl. 27) which are reproduced with a unique fidelity to nature showing us the animals as they are to this very day. But also the birds are reproduced with such fidelity, that we are able to determine with certainty the species as the *Anas acutus*, the *Bernacle* goose the cranes (*Grus cinerea*); the wagtail (ur) (*Motacilla alba*); the same birds which are still common in Egypt either the whole year round or which to this very day, after the passage from the high North, may be seen lying upon the waves of the Nile. I refer the reader especially to: *Das Grab des Ti*, Taf. 129; to LEPSIUS: *Pyramiden von Giseh*, Bd. 3, Grab 73, and from Saqara and to BENI HASSAN I, Pl. 27, a. o.¹⁾

4. The faunas of old islands differ considerably from that of the adjacent continents; on the other hand if the isolation, geological speaking, is of a rather new date (pliocene or quaternaire) the faunas between the islands and the continents are almost identical. (GERMAIN 1924 p. 129, HESSE a. o.)

5. All domestication of our animals, in the case of several of them carried on through thousands of years, has all in all never been able to create new species, only races and varieties. It is of the greatest interest, as LAVALLE (1911 p. 918) has pointed out, to see how the breeders have throughout a period lesser than a century unswervingly been able to model out a race, as the English game-fowls; on the other hand new species have here as nowhere been produced.

¹⁾ For assistance with regard to this literature I am in great debt to Dr. H. O. LANGE.

Now if these facts are duly considered, how then can we expect that in the poor miserable space of time used for the experiment, an immeasurable glimpse of eternity, we should be able permanently to influence the germ plasm? Are our unsuccessful attempts in this direction proof of the immutability of the germ plasma and of discontinuity in evolution?

I know very well that an objection will be raised. Owing to the lively propagation of Daphnids, Rotifers and Infusoria it is possible during a few years to try variations in outer conditions upon as many generations as organisms, especially the higher animals, have traversed during the last 4—5000 years. This is quite right, but in my eyes one of the great sources of error with regard to all one-sided laboratory work lies just here. Because a condensed outer factor in the course of a few years in the laboratory is unable to influence the germ plasma, the students of heredity are inclined to suppose that the result would be the same if the organisms in Nature through thousands of years are influenced by the same outer factor, either invariable in strength or during this time slowly working its way up to the degree of intensity used in the laboratory experiment. When the students of heredity on the basis of experimental work regard themselves as entitled to declare that acquired characters cannot be inherited, they seem to take just that for granted of which we have not the slightest knowledge at all: viz. the interaction between labile periods, number of generations, time and the degree of intensity with which the outer factors act.

It is often maintained by the students of heredity that if it is impossible to place any confidence in the supposition that modification of germ plasm caused by variations in outer conditions take place, this is due to the fact that it is at variance with all that the last twenty years' study of heredity has brought to light. Indeed this is most probably right and on account of this fact they have in ever-increasing degree scorned the Lamarckians and Darwinists. Though their own laboratory studies with regard to the question of the origin of species have only brought science a very modest cock's stride forward, they have postulated that Darwinism had nothing to do with natural science. From a biological point of view it may be permitted to maintain that studies on heredity, which without due regard to the results of morphology and palæontology and their working methods, overstep the natural limits of hereditary work and try to elucidate the origin and development of species in Nature, are at bottom unscientific. —

Through accumulations, invisible to the human eye, over vast periods of time, regular variation in outer conditions have influenced and still influence the germ-plasma of the species. The great epochs in the history of our globe accomplished in short periods, geologically speaking, have brought whole faunas into mutable periods, the result of which is either extinction or relatively sudden immense development of new types, rarely conservation of old ones: survivals, relics; in other words extinction for all those types whose germplasma has by accumulation been influenced in the direction opposite to the new life conditions, and life in new forms

for those which had been influenced in accordance with them. Between these periods owing to use or non-use of organs, the further development of which was either supported or stopped by selection, the species may be split up into varieties and "petits espèces", formfixed at all events under the same outer conditions. All experimental hereditary study should be restricted to this last part of the evolution; by trying to go further it oversteps its limits of competence. —

In the biological literature from the last years we find the same thoughts but merely expressed in a different way. GOODRICH (1924 p. 153) "Every theory of evolution must be tested by the results of palæontology; no conclusion can be accepted which is inconsistent with them." —

No dogma can be more in disaccordance with the palæontological data than that of discontinual origin of mutations. I only refer to OSBORN: *L'origine et l'évolution de la vie* 1921 a. m. o. It would take us far afield here to go into details. Quite correctly GOODRICH (1924 p. 122) says: "Indeed we can hardly imagine that the complex adaptations so commonly found, the marvellous cases of protective resemblance between organisms and their surroundings, and similar developments, could have arisen otherwise than by the accumulation of small differences step by step."

I cannot see but that if we regard the mutations as prepared and determined by fluctuations and modifications, we have in the main the explanations of from where the mutations derive, how they originate and how they develop. With this apprehension in view it will be understood that it is impossible to place any confidence in the presumed sharp limits between variations due to outer and inner conditions. In every moment of its life an organism is a historical product. The same variation which to day is produced by inner conditions, was in the past produced by outer ones, in the meantime carried down and preserved in the germplasma; or as GOODRICH 1924 p. 52 says: "The characters of an organism are but the sum of its past responses". The basis of the whole apprehension is the supposition that the environment through the soma may be able to influence the germcells. Scientists who are unable to attach any significance to all negative results of all experimental work upon this point, from their own studies and whole scientific training very often know a number of phenomena which strongly seem to corroborate this view. I shall here not enter into details but only call attention to the fact, that the number of scientists who in the last few years, in very different fields of biological sciences are inclined to admit the necessity of this theory seems to be steadily increasing. I need here only refer to HILZHEIMER: *Natürliche Rassen-geschichte der Haussäugetiere* 1926 p. 29—31 and in this connection GOODRICH (1924 p. 118). CUÉNOT: *L'adaptation* 1925 chap. *Mutationisme* p. 91. DÜRKEN: *Allgemeine Abstammungslehre* 1924 p. 171. ALVERDES: *Rassen- und Artbildung* 1921 p. 84; MEISENHEIMER 1923 p. 114 a. m. o. Also GUYÉNOT (1924 p. 46) is ready to admit the possibility that the environment through the soma may be able to influence the germcells. He says as follows: "Peut-être un jour pourrions-nous rattacher

les mutations à des modifications du milieu; si l'on prend ce terme dans son sens le plus large, c'est-à-dire si l'on considère que les cellules voisines, le reste du corps, représentent le milieu pour les cellules germinales qui ont été le siège d'une mutation?"

Supposing that the great rules which govern all life in Nature are the same which also govern Man, his culture, his religions, his history, his whole ideal world, it would in my eyes be extremely fatal for the result of the last twenty-five years' study of heredity if the doctrine relating to discontinual development could not be applied to these vast domains of human knowledge. But where is the historian or philosopher who will maintain that historical events, great or small, or human ideas, arise at haphazard without any connection with earlier events or ideas, with space and time, with environment etc. and who will deny the significance of accumulatory forces in these domains? (See also GOODRICH 1924 p. 171 Chap. Psychology and the evolution of Intelligence. "The laws of variation, inheritance and natural selection hold good in mental as in material evolution.") —

As far as I can see, the dogma of discontinual development is totally out of harmony with the results relating to the studies of and conception of the form series. Others have arrived at quite the same result, especially EKMAN; he has dissented very vigorously from the theory of discontinual development. As a result of his explorations he maintains that: "Im Wesen des Lebendigen liegt genotypische Verschiebbarkeit; genotypische Festigkeit ist nur scheinbar und zufällig". Quite like PLATE (1913 a p. 473; 1913 b p. 76) he (p. 67) urges that the term mutation has had a very peculiar development; "Anfangs trat sie durch ihre Hervorhebung des sprungartigen im Ausbildungsvorhang in scharfem Gegensatz zu den früheren Evolutionstheorien. Alsbald erwies es sich aber, dass die mehr auffälligen Mutanten zu den Seltenheiten gehören; man lenkte die Aufmerksamkeit immer mehr von der Vorstellung der sprungweisen Entwicklung ab . . . bis es endlich heisst, dass jede erbliche Abänderung eine Mutation sei, nur mit dem Vorbehalt, es handle sich nicht um Bastardierung. Damit ist aber das Neue in der Mutationstheorie gänzlich aufgehoben. Der Name Mutation ist eigentlich das Auffälligste, was die Theorie von ihrem Anfangsstadium bis jetzt gebracht hat." With regard to the question relating to continual and discontinual development EKMAN (1913 p. 101) maintains: "Sie basiert nicht auf dem Nachweis eines tatsächlich vorhandenen natürlichen Kontrastes, sondern auf einer verfehlten theoretischen Konstruktion". —

Not until after I had formed my opinion with regard to the form series of the Daphnids did I become acquainted with the papers of EKMAN, PLATE, STANDFUSS, SEMON. I confess that the views at which I arrived were in accordance with these authors.

The doctrine of discontinuous development is unable to give us any apprehension of the harmony in Nature; what it can do is merely to unveil the secret of lawlessness, with which Nature has nothing to do. In the chaos which discontinually originating mutations would create no selection would be able to bring order and no formseries would be developed.

If it be maintained that all hitherto known mutations by no means are direction-determined and to a much higher degree may be said to be the opposite, two things must well be remembered: The one is that all hitherto well explored mutations derive from work in the laboratories and are treated there. Secondly, as is often admitted, that almost all these mutations, deriving from laboratory work, if transferred to Nature, cannot live there. As well known MORGAN maintains that none of his 400 mutations of *Drosophila* if transferred to Nature would be able to issue victorious from the struggle for existence. (CUÉNOT: 1925 p. 94) How then it is possible to use all these poor creatures as support for the conception that mutations produced in Nature are not direction determined is more than a biologist can understand. As far as I can see, just this use of the laboratory mutants as proof of the theory that evolution should go on discontinually is one of the best proofs of what irrelevancies onesided laboratory work can lead scientists to and how far from the way of truth the "exact" study of heredity may take its devotees. And how they only for a moment could expect that all these miserable creatures, with regard to vitality not differing very much from those "homunculi", which the sorcerers of a past time supposed they could create chemically, in the long run should be able to subvert the combined results of all that Palæontology, Embryology and Morphology has built up in more than half a century, is incomprehensible to all those naturalists who have studied Nature not onesided only in laboratories, but also and mainly in Nature itself.

As far as I can see, it has been shown that in the form series, wherever they are studied, the systematic value of the units is quite different. Some units are unmistakable modifications, others well defined species or genera. The units are not discontinually thrown out pell-mell among each other, but vary regularly with regard to characters according to regular variations in outer conditions, variations in the bearing power of the fresh water, in salinity, in light, in the degree of moisture, in nourishment, characters which may be regarded as adjustments to these variations, and which increase in strength in accordance with these variations in the outer medium.

Up to a certain point of time and a certain degree of pressure from without, the species are so to speak able to remain quiescent. But the uninterrupted, immutable influence from without, acting perhaps through thousands of years, has imperceptibly changed the germplasma; the result of which is that countless individuals simultaneously come into a mutable period. And suddenly as a result of an accumulation carried on over immense spaces of time a new species is born. If species can die, they may also have their period of propagation i. e. their mutable periods. Variation in outer conditions is the impulse arriving from without; it drives the species out of their periods of balance and equilibrium; representing as it were the virile element. But only in certain periods in the life of the species and as a result of the combined action of possibilities of combinations in outer and inner conditions does a conception take place and new species arise; to the mastering of this har-

mony we shall most probably never attain. At all events at this very moment we are unable to create mutations, but as the breeders do through crossings and variation of habitat we may perhaps be able to prepare their origine. That crossings between units of a higher order may be that which actually gives rise to total mutations may be possible, but that this as a rule should be primus motor and variations in the environment should have no significance or mere play a rather subordinate part I regard as highly improbable.

Where new species arise, they look like mutations to the human eye; it seems as if the development goes on discontinually, they have the stamp of the total mutation (Lamarckiana type), but nevertheless they are in the highest degree determined by variations in outer conditions. They spring forth fully armed like Pallas Athene from the head of a Zeus. With their appearance directly selection has nothing to do, but when they appear in a population, they act selectively upon the environment. When we have hitherto spoken of selection as the great exterminator and chucker out of all feeble, half done, and badly done work, it was always as if selection was regarded as a sort of supernatural entity, the results of whose work we could actually see, though never its working method.

But just these new species derived from a remodelling of the genotype act as those factors which at one sweep, their direction suddenly determined, have forced the evolution a great step forward, far beyond the power of adaptation of the primitive species. They act as exterminators of all the last, feeble, or, at least not very vigorous, attempts at the extreme limits of the range of variations of the species to accommodate itself to the ever-increasing demands from without. It is the new species which, though they may well be said to go on where the predecessor stopped, exterminate the intermediate forms, the missing links, with the result that where two species meet at the line of demarkation, they stand rather sharply against each other. The phenomenon is related to the results mentioned by the breeders of domesticated animals: that animals which may be designated as mutations are provided with a very pronounced "Vererbungskraft" (HILZHEIMER 1926 p. 29).

Sooner or later the new species itself will come under the law of transformation; it begins to vary in accordance with the primary species, spreads over areas where this could not accommodate itself, but which are in accord with its own constitution. And if the variations in outer conditions are augmented in the same direction, a time will come when this too either owing to overspecialisation will be destroyed or gets its range of variation "blown up" by the accumulation and a new species is produced. But wherever mutations are to promote evolution they must most probably be combined with wanderings and isolation. This again will be dependent upon variations in behaviour, in the psychology of the organism. It will be understood that selection during these processes acts not only as the great exterminator but also as the promotor of evolution.

Quite correctly HUGO DE VRIES has said that the mutable periods are much shorter than those in which the species are at rest; and that between the mutable

periods there may be thousands of years. The last great epoch in the history of our globe was the Ice Age. While acknowledging the Ice Age as a species-varying factor we must not forget that in ever-increasing degree voices are heard, which maintain that what new material has appeared, is in the main only modifications, new combinations, Phænotypes, and that the genotypic changes are all in all of rather a moderate kind. If therefore many students of heredity will maintain that the germ plasma cannot be modified by outer conditions, that acquired characters are not hereditary, they may be right for that period of the history of the earth in which we now live, but if they regard this dogma as the norm according to which the species have been developed from the beginning till our day, not considering the enormous significance of the accumulation for the germ plasma, they are by no means right in my eyes. And if the exact students of heredity demand that in order to give credence to the views set forth in this work, they should be able to transform in the laboratories one *D. longispina* race into another, they are wrong in my eyes. Related thoughts we find by LOTSY (1916 p. 136).

We cannot expect, however much we exaggerate conditions in the laboratories in the outer medium, to break the resting periods of the organisms and carry them into labile periods. I know very well that it seems as if this has been really done several times, but failures in this respect have no significance at all. What a species has worked at for thousands of years, cannot be wiped out in the course of some years.

However it must never be forgotten that JOHANNSEN has more than once maintained in his work that the outer conditions "Lebenslagefactoren" (1909 p. 446, 449, 464) may have a rather considerable influence on the greater or smaller percentage of mutations; especially copious variations in nourishment are said to be of significance. It is, however, as if he does not attach much weight to this. For that very reason, I suppose, JOHANNSEN is forced to arrive at the often cited and in their scientific honesty to unusually fine words: "Leben kann sich offenbar nur als Komplexerscheinungen manifestieren. Die Analyse des Lebens führt zum Tode — und Synthese des Lebens wird uns wohl nie gelingen." (1909 p. 439). —

I do not share the views of JOHANNSEN. Nowhere is the synthesis of life more sublimely manifested than in the ever-increasing perfection of the organism, in the ever-increasing development from lower to higher stages. Just this evolution is often said to be totally inconceivable under whatever aspect we try to understand it. On the other hand, if we suppose that this evolution has been going on alongside with a greater and greater differentiation in the outer medium, in the life conditions from the earliest epochs of our globe till the present day, if we remember that the use or non-use of organs and qualities are governed by psycho-physiological forces, mnemonic phenomena, if we compare the results of all our study of living organisms with those derived from the study of inorganic life, especially with those obtained by the study of the history of our globe; if we remember on the one side that all that an Ice Age has produced is only small variations in the germ plasma, on the

other hand, that these variations are realities, why then should we not also be able to place confidence in the thought that evolution from the first moment when the first vestiges of organic life appeared on our globe has worked along with and in accordance with those forces which made our globe more and more habitable and slowly but in ever-increasing degree differentiated the life conditions of all organic life; owing to this differentiation and along side with it the differentiation of the forms of life went on. We may abandon the conception of an organism as a machine and the doctrine of sharp limits between an organism and its environment. It must well be remembered that the solution of all the questions relating to the origin of species, which are raised again and again and always will be raised, is most probably to be found in those strata of our globe which, owing to their construction have been unable to preserve petrifacts. Furthermore these petrifacts themselves were most probably in a condition with regard to their skeletons, which made preservation an impossibility.

If we try to understand the evolution of species and the synthesis of life, we cannot solely follow those lines which the modern exact studies on heredity regard as the only safe ones. In these fields the experiments are of very small significance, at all events experiments that have failed mean very little. When BAUR (1919 p. 348) transfers JOHANNSEN'S dictum with regard to the study of heredity: "Treatment, mathematical, philosophical and phantastical may be disputable, what we want much more than is commonly admitted, are well analysed pure and clear elementary premises" to the problem of the origin of species, I cannot follow him. BAUR'S conclusion: "Also viel mehr Experimentieren und weniger Theoretisieren ist die Parole für die nächste Zeit" is here not in accordance with my views.

The problem of the origin of species is a problem of observation of the living organisms in Nature itself combined with reflexion based upon anatomical-morphological studies, palæontological data and with due consideration of psycho-physiological phenomena and hereditary studies. Against all those who suppose that all questions with regard to the origin of species can only or mainly be promoted by means of experiments, numbers, and figures, and who seem to suppose that only those explorations which have as motto GALILEI'S dictum: "Measure all that is measurable and make it measurable if it is not" can be called exact, it is allowable to maintain another view. In biological investigations, in investigations relating to the evolution of species, figures place boundaries where no boundaries exist. They control our thoughts but also prevent their flight; they give an investigation an appearance of accuracy which is not always well deserved; they make the results more marked than is justifiable, and give them a momentary clearness which hides all the tangles behind; we shall never be able to arrive solely by any amount of measuring or experiments at any apprehension of the origin of species. In these fields of research only that life work has value in which there is found some trace of the — immeasurable.

Almost half a year after this paper was sent to press and after the last sheets were printed, I became acquainted with the works of HALDANE (1917) and RUSSEL (1924). I regret very much that these works have been quite unknown to me. In spite of the different store of knowledge, some of the leading thoughts are the same as are pointed out in this work. In HALDANE'S work I take the liberty mainly to call attention to Chap. IV: Organic regulation. HALDANE maintains that living organisms cannot be regarded as "ordinary machines". An organism possesses an active adaption, without that everything would tend to go from bad to worse as is just the case with an untended machine. The tissues adjust themselves to variations in outer conditions; the adaptation is first functional, later on structural, and if the structures are destroyed, phenomena of vicarious functions may occur. From a purely physiological standpoint memory may be regarded as a phenomenon of the same nature as adaptation (effects of practice in the carrying out of any operation). "In a living organism the past lives on in the present and the stored adaptations¹ of the race live on from generation to generation, waking up into response when the appropriate stimulus comes, just as conscious memory is awakened.¹)

We find the same related thoughts advanced in Russel's excellent work: The study of living things. In his chapter: "Response by change of form" he points out that the term of behaviour on the part of the organism is not invariably muscular movement or chemical responses; it may also be what he calls of morphoplastic nature. The morphoplastic responses are not carried out by an instrument already present, the instrument or organ is found in the course of the response, either as a new formation from undifferentiated living substance or by the modification of some existing organ (the ad hoc formation of organs in Amoeba and Pelomyxa). In higher animals organs are found ad hoc but remain as permanent structures. The line between behaviour response and morphoplastic response is hard to draw. The structural modification entailed in behaviour response is as a rule rapid and transitory but usually leaves a slight modification; the structural change implied in morphoplastic response is slower and more permanent, and may result in a radical transformation of the existing organ. Behaviour action is as a rule prompt and rapid, morphoplastic response is very much slower.

According to Russel the problems of development and heredity should be treated from a functional point of view; a purely material view of the processes leads to nothing; heredity and development cannot be filled into the mechanistic schemes. The relations between the genes and the adult characters whose development appears to be in some way dependent upon these genes are quite obscure, and the theory of genes when applied to the problems of development at our present stage of knowledge is therefore unhelpful.²) According to Russel, development is a functional

¹) Italicised by me. See pag. 234.

²) We find related thoughts in the very suggestive discourse by Křiženecký held in Naturf. Verein in Brünn 1922 where he sharply distinguishes between the real, exact Mendelismus and the theoretical "neomendelistic" one: "die Lehre von den Genen als den entwicklungsgeschichtlichen Grundlagen der Merkmale".

differentiation. This functional differentiation proceeds in each species along definite lines determined by heredity. Development is, however, not entirely automatic; for the developing embryo may exhibit considerable powers of self-regulation; furthermore it does not as a rule take the straight path from the simplicity of the egg cell to the complexity of the adult, but follows an indirect course which hints back at the evolutionary history of the ancestors. In the earlier stages of development form precedes function; later on as development proceeds, the full differentiation of the organs becomes dependent upon their function. The functional method is forced to use the mnemonic theory: Organs originally found in response to particular environmental conditions, may in the course of generations gradually lose their dependence upon the functional stimulus and appear in ontogeny in response to an associated stimulus or in the absence of any stimulus at all. "The mnemonic theory in this way allows for a transmission of acquired characters the evidence for which appears of late years to be increasing." ¹⁾

As well known, during the last twenty years the Cladocera and almost only the genus *Daphnia* have been very much used for hereditary studies; by no one more than by WOLTERECK. Mainly with regard to the final results of his studies, at all events as they are hitherto known, it must be admitted that WOLTERECK would most probably have been able to deepen his view and ground his suppositions more thoroughly if he had taken more notice of the form series and their origin. As far as I can see it is just to this lack of knowledge that it is due, that the author, regarding variation in nourishment as causing the seasonal variations, has confounded the means with the goal. From this again the theory of the buoyancy organs as means to keep the organisms in special strata in which their nourishment would be found, has its origin. Finally this last supposition has taken the author to the theory of the position and the significance of the Nannoplanton and the interdependence between it and the Zooplanton, which may be designated as a theory lacking all scientific foundation. The question as to how variations in outer medium, i. e. variations in the amount of energy, are able to influence the formation of species WOLTERECK answered in the following way. Without prediction of any kind variations in the outer medium influence all organs which are subject to variation in blood pressure and blood nourishment. Variations in the amount of energy, however, can never explain the disproportional prolongation of special organs (crustæ, thor's). According to WOLTERECK this is partly due to selection and partly to a disproportional "labilität" of the special regions of the body. Even if a onesided and progressive augmentation of an organ cannot be caused by blastovariants deriving directly from variation in the outer medium and from the influence of a now augmenting, now smoothing hybridisation, it may be regarded as highly probable that in this way a very rich material for selection may be prepared. Just these two factors, blastovariation and hybridisation between the

¹⁾ Italicised by me. See pag. 204.

lines, are the primary and secondary causes of the phenomenon that differences in norm are present in all populations. If now it were possible to show that the "Merkmaländerungen" which go on tending in a quite distinct direction suitable for the purpose (e. g. regular prolongation of the crista, i. e. slow and constant augmentation of the communicated milieu energy in favour of the formation of the crista) really were useful for the organism, it would be possible to ascribe the result to selection. Now WOLTERECK maintains that even the slightest possible variations which in any way influence the position of the centre of gravity or the "Steuerorgane" may really be of significance — bad or good — for the organism, in WOLTERECK's opinion because, by horizontalising the swimming tracks, they will keep them in their strata of nourishment.

With regard to the "localisierte Labilität" i. e. the phenomenon that the different parts of the body show a different tendency to variation W. distinguishes between those which do not exceed the reaction norm and the blastovariants or hereditary variants. —

To the first-named belong the spontaneous oscillations, the periodical variation and the specific sensibility to outer conditions. To the last-named category belongs the sensibility of the crista to variations in the outer medium, in the first place variations in nourishment influencing the blood pressure; this influence may be shown also for the young ones developing in the brood room (W.-L.) and for "die im Ei ruhende Geschlechtlichkeit" of the following generation (Præinduction of WOLTERECK). To this belong mainly the length of the crista, the length of the rostrum, the length of the spina and the amount of pigment in the pigment spot. WOLTERECK maintains that upon these points he has produced hereditary transgressive variations; upon this point W. promises new publications; what has hitherto been published upon that subject is rather problematic, at all events the results are exceedingly small.

The origin of new species has its starting point in disproportional variations in the body which arise from spontaneous reactions, deriving from variations in the outer medium; these spontaneous reactions will then through selection be fixed as norm reactions, which later on stiffen to compulsory reactions. The buoyancy organs, the prolongation of special parts of the body, may partly be fixed specific characters as is the case in the genera *Leptodora* and *Bythotrephes*, partly be variable ones, determined by the milieu and time (*Daphnia*, *Bosmina*).

It is easily seen that, with regard to the conception of the races of the Genus *Daphnia*, WOLTERECK and I have in many respects from different ways reached similar results. In my opinion all that WOLTERECK has written on the so-called "localisierte labilität" is not scientifically grounded and only a rewriting of the fact that we do not know anything. When further WOLTERECK maintains "that if "Merkmalsänderungen" tending in a quite distinct direction suitable for the purpose (i. e. slow and constant augmentation of communicated milieu energy in favour of the formation of the crista)" would really be useful for the organism, it would

be possible to ascribe the result to the selections, I agree with W. with regard to the races, but in the species I see mutation as a result of an accumulation.

If we transfer the results of WOLTERECK and his mode of expression to the newly published explorations, we shall arrive at the following results.

With the retreating ice, the decreasing bearing power of the fresh water, combined with an increasing amount of nutritive material, the spontaneous reactions appeared. Through selection they were transformed into norm reactions arranging themselves in form series. That all these hereditarily fixed reaction norms connected by immeasurable transitional stages, from biotype to biotype, in their occurrence in Nature dependent upon regular variations in the outer medium, should occur without connection with outer factors, without transgressions from soma to germ plasma may, as far as I can see, be regarded as an impossibility. They may be referred to idiopinetic processes from which the mutation originated. —

Because WOLTERECK has taken no notice of EKMANN'S and my paper and underrated the significance of the form series he is forced to give a very insufficient explanation of the fact that in some of the Cladocera the so-called buoyancy organs are fixed species characters (*Leptodora*, *Bythotrephes*) in others (*Daphnia*, *Bosmina*) not, being here only left at the stage which WOLTERECK calls norm reactions. According to WOLTERECK this is supposed to be due to the physiological differences in the use of the buoyancy organs (Richtungsorgane WOLTERECK). In my eyes this is due to quite another fact.

The plankton of our fresh water lakes consists of perennial and periodical plankton organisms; the periodical ones are almost all summer forms immigrated long after the melting period of the ice, very old forms which have not been under the influence of the periods after the melting of the ice; the perennial plankton has originally been able to accommodate itself to great differences with regard to temperature. It has so to speak followed hot-foot upon the retreating ice, has accustomed itself to very low temperatures in that remote period, for many of its species mainly belonged to small waters. A tendency to pelagic life in the larger water masses arose; with the amelioration in outer conditions increasing, a higher buoyancy power was required, and precisely in that variation in the outer medium we find the race-forming factor for many of the perennial plankton organisms, race formation among the periodical ones being unknown. When this race formation has not gone beyond the stage of norm reactions, this is due to the fact that, when the milieu during winter again shows conditions of temperature related to those of the Ice Age, the species revert to the forms they had during those remote times, and which are the same under which they live the whole year round to this very day in the arctic region. The great regular variation in climate from the melting period to our day has been able to produce "norm reactions" but no fixed species characters.

LIST OF LITERATURE

A * before the name will say that the work has not been consulted.
Literature after 1924 has only rarely been used.

1921. ALVERDES, F. Rassen und Artbildung. Berlin.
1911. BACHMANN, H. Das Phytoplankton des Süßwassers mit besonderer Berücksichtigung des Vierwaldstättersees. Mitt. der Naturf. Ges. Luzern **6** Heft p. 5.
1914. — Das Nannoplankton. Naturwissenschaftliche Wochenschrift **13** p. 1.
1921. — Beiträge zur Algenflora des Süßwassers von Westgrönland. Mitteilungen der Naturforschenden Gesellschaft Luzern Heft 8 p. 4.
1908. BALLY, W. Der Obere Zürichersee. Archiv f. Hydrob. **3** p. 113.
1913. BANTA, A. M. Selection within pure lines of *Daphnia*, Science n. s. **37** p. 272.
1914. — One hundred parthenogenetic generations of *Daphnia*, without sexual forms. Proc. Soc. Exp. Biol. M. **11** p. 180—182.
1915. — The effects of long-continued parthenogenetic reproduction (127 generations) upon *Daphnids*, Science, n. s. **41** p. 442.
1919. BAUR, E. Einführung in die experimentelle Vererbungslehre. Berlin.
1895. BEDRIAGA, J. VON. Die Lurchfauna Europas. Bull. de la Soc. impér. des Naturalistes. Moscou. N. S. **10**.
1913. BEHNING, A. Studien über die vergleichenden Morphologie sowie über die temporale Lokalvariation der Phyllopodenextremitäten: Intern. Rev. Biol. Suppl. **4** p. 1.
1914. BEHRENS, H. Die vertikale Verbreitung des Crustaceenplanktons. Königl. Inst. f. Meeresk. Berlin. Seenstudien.
1892. BIRGE, E. A. List of Crustacea *Cladocera* from Madison. Wisconsin Academy Sc. **8**.
1893. — Notes on Cladocera. III. *ibid.* **9**.
1911. BIRGE, E. A., and JUDAY, C. The inland lakes of Wisconsin. Wisconsin Geological and Natural History Survey. Bull. **22**.
1892. BOAS, I. E. V. Organe copulateur et accouplement du Hanneton. Oversigt over det Kgl. Vid. Selsk. Forh.
1906. BORCHERDING, F. *Achatinellen*-Fauna der Sandwich Insel Molokai. Chun: Zoologica **19** H. 48 I—II.
1902. BREHM, V. Zusammensetzung, Verteilung und Periodicität des Zooplankton im Achensee. Zeitschr. d. Ferdinandeums III. F. Innsbruck **41** p. 1.
- 1909a. — Charakteristik der Fauna des Lunzer Mittersees. Internat. Revue **2** p. 741.
- 1909b. — Über die Nackenzähne der Daphnien. Internat. Revue **2** p. 749.
1923. BREHM, A. Die Vögel. Bd. V. Bibliographisches Institut.
1923. BUMM. Grundriss zum Studium der Geburtshülfe.
1899. BURCKHARDT, G. Faunistische und systematische Studien über das Zooplankton. Revue Suisse de Zool. Genève **7** p. 353.
1900. BURCKHARDT, G. Quantitative Studien über das Zooplankton des Vierwaldstättersees. Mitt. d. Naturf. Gesell. Luzern **3** p. 1.

1914. COLDITZ, F. V. Beiträge zur Biologie des Mansfelder Sees. Zeit. f. wiss. Zool. **108** p. 520.
1916. CRAMPTON, H. E. Studies on the variation, distribution and evolution of the genus *Paratula*. Carnegie Institution Publ. 228.
1925. CUÉNOT, L. L'adaptation. Encyclopédie scientifique. Paris.
1895. v. DADAY, E. Beiträge zur Kenntnis der Plattensee-Fauna. Math. u. naturw. Ber. aus Ungarn **3** p. 179.
1897. — Crustacea: Resultate der wissenschaftlichen Erforschung des Balatonsees **2** Teil 1 Sec. 9.
1907. — Plancton-Tiere aus dem Victoria Nyanza. Zoolog. Jahrb. **25** p. 245.
1912. DIEFFENBACH, H., & SACHSE, R. Biologische Untersuchungen an Rädertieren in Teichgewässern. Intern. Rev. Biol. Suppl. **3** p. 1.
1924. DÜRKEN, B. Allgemeine Abstammungslehre. Berlin.
1904. EKMAN, S. Die Phyllopoden, Cladoceren und freilebenden Copepoden der nord-schwedischen Hochgebirge. Zool. Jahrb. **21** Abth. Syst.
1913. — Artbildung bei der Copepodengattung *Limnocalanus* durch akkumulative Fernwirkung einer Milieuveränderung. Zeit. f. induktive Abstammungs- und Vererbungslehre **11** p. 39.
1906. ESCHERICH, K. Die Ameise. Braunschweig.
1922. FABRE, J. *Mantis religiosa*. Skik og Brug hos Insekterne p. 53.
1901. FISCHER, E. Experimentelle Untersuchungen über die Vererbung erworbener Eigenschaften. Allg. Zeitschr. f. Entom. **6** p. 49, 363, 377; **7** 1902.
1893. FORBES, S. A. A preliminary Report on the aquatic invertebrate fauna of the Yellowstone park. Bull. of the U. S. Fish Commission for 1891. Washington p. 207.
1874. *FOREL, A. Fourmis de la Suisse. p. 388.
1913. FREIDENFELT, T. Zur Biologie von *Daphnia longiremis* G. O. Sars und *Daphnia cristata* G. O. Sars. Internat. Revue **6** H. 2—3 p. 229.
1913. v. FRISCH, K.,—KUPELWIESER, H. Über den Einfluss der Lichtfarbe auf die phototaktischen Reaktionen niederer Krebse. Biologisches Centralblatt **33** p. 517.
1917. FRITZSCHE, H. Studien über Schwankungen des osmotischen Druckes der Körperflüssigkeit bei *Daphnia magna*. Internat. Revue **8** p. 22.
1915. GANDOLFI-HORNYOLD, G.,—ALMEROETH, H. Mitteilung über die Verteilung von *Daphnia hyalina* Leydig im Genfer See (Petit. Lac). Intern. Revue **7** p. 426.
1911. GERHARDT, U. Studien über die Kopulation einheimischer Epeiriden. Zool. Jahrb. Syst. **31**.
- 1913—1914. — Copulation und Spermatophoren von Grylliden und Locustiden. Zoolog. Jahrbücher. Abt. f. System. 1913 **35** p. 415. 1914 **37** p. 1.
1924. GERMAIN, L. La vie des animaux à la surface des continents. Paris.
- 1910—1914. GODLEWSKI, E. Physiologie der Zeugung. Winterstein: Handbuch der vergl. Physiologie **3** p. 457.
1923. GOLDSCHMIDT, R. Einführung in die Vererbungswissenschaft. Leipzig.
1924. GOODRICH, E. S. Living organisms. Oxford.
1914. GREESE, B. Einige Beobachtungen über die Variabilität der Endkrallen bei *Daphnia pulex*. Intern. Revue Biol. Suppl. **6** Ser. p. 1.
- 1913a. GRUBER, K. Studien an *Scapholeberis mucronata*. O. F. M. I. Beiträge zur Frage der Temporalvariation der Cladoceren und ihrer Beeinflussung durch das Experiment. Zeitschrift für induktive Abstammungs- und Vererbungslehre **9** p. 301.
- 1913b. — Das Problem der Temporal- und Lokalvariation der Cladoceren. Biologisches Centralblatt **33** p. 455.
1905. GULICK, J. T. Evolution, Racial and Habitual. Carnegie Institution of Washington Publ. No. 25.
1924. GUYÉNOT, E. L'hérédité. Encyclopédie scientifique. Paris.

1917. HAACK, M. Zur äusseren Morphologie einiger Daphniden. Dissert., Intern. Revue 8 p. 338.
1920. HABERBOSCH, P. Die Süßwasser-Entomostracen Grönlands, eine faunistische, oecologische und tiergeographische Studie. Zeitschrift für Hydrologie. 1. Jahrgang p. 136, p. 245.
1909. HAECCKER, V. Die Radiolarien in der Variation und Artbildungslehre. Ergebnisse d. Deut. Tiefsee Expedition 2.
1921. — Allgemeine Vererbungslehre. Braunschweig.
1921. * HAGEDORN, A. L. and A. C. The relative value of the processes causing evolution. The Hague. After Turesson.
1921. HANIEL, C. B. Variationsstudie an timorizischen *Amphidromus*-arten. Zeitschr. f. induktive Abst. 25.
1918. HARBITZ. Lärebok i Retsmedicin.
1915. HARTMANN, O. Studien über die Cyclomorphose bei Cladoceren. Archiv f. Hydrob. und Planktonkunde 10 p. 436.
1916. — Ueber den Einfluß der chemischen Beschaffenheit des Mediums auf die Gestalt von *Bosmina longirostris*. Archiv f. Entwickl. mech. 42 p. 208.
1920. — Studien über den Polymorphismus der Rotatorien mit besonderer Berücksichtigung von *Anuræa aculeata*. Archiv f. Hydrobiologie 12 p. 209.
1914. HASEBROCK, K. Ueber die Entstehung des neuzeitigen Melanismus der Schmetterlinge. Zool. Jahrb. Syst. 37.
1904. HENNEGUY, J. F. Les Insectes. Paris.
1917. HERR, O. Die Phyllopodenfauna der preussischen Oberlausitz und der benachbarten Gebiete. Dissert.
1916. HERTWIG, O. Das Werden der Organismen. Jena.
- 1910—1914. HESSE, R.-DOFLEIN, F. Tierbau und Tierleben. Leipzig und Berlin.
1924. HESSE, R. Tiergeographie. Jena.
1917. HEUSCHER, H. Das Zooplankton des Zürichsees. Archiv f. Hydrob. u. Planktonkunde. Plöen 11 p. 1, p. 153.
1866. HILGENDORFF, H. *Planorbis multiformis* in Steinheimer Süßwasserkalk. Monatsber. d. königl. Academie d. Wissensch. Berlin p. 474.
1901. — Der Übergang von *Planorbis multiformis-trochiformis* zum *oxysternus*. Archiv f. Naturges. 67 Suppl. p. 331.
1919. v. HOFFSTEN, N. Ärfllighetslära. Stockholm.
1906. HUITFELD-KAAS, H. Planktonundersøgelser i norske Ferskvande. Christiania.
1908. ISSAKOWITSCH, A. Es besteht eine zyklische Fortpflanzung bei dem Cladoceren aber nicht im Sinne Weismann's. Biol. Centb. 28 p. 51—61.
1900. JENSEN, A. S. Studier over nordiske Mollusker. I. *Mya*. Vidensk. Medd. Naturh. Foren. København p. 133.
1909. JOHANNSEN, W. Elemente der exakten Erblchkeitslehre. Jena.
1906. KEILHACK, L. Zur Biologie des *Polyphemus pediculus*. Zool. Anz. 30 p. 911—912.
- 1909a. — Phyllopoda und Cladocera in: Brauer: Die Süßwasserfauna Deutschlands.
- 1909b. — Zur Bedeutung der Generationszyklen bei den Cladoceren. Intern. Revue 2 p. 238.
1908. KLAUSENER, C. Die Blutseen der Hochalpen. Intern. Revue 1 p. 359.
1924. KORSCHULT, E. Bearbeitung einheimischer Tiere: *Dytiscus marginalis*. Leipzig.
1908. KRÄTSCHMAR, H. Ueber den Polymorphismus von *Anuræa aculeata*. Intern. Revue 1 p. 623.
1913. — Neue Untersuchungen über den Polymorphismus von *Anuræa aculeata*. Intern. Rev. 6 p. 44.
1924. KRÍŽENECKÝ, J. Die heutige Vererbungswissenschaft und ihre neue Aufgaben. Revista di Biologia 6 Fasc. 1 p. 1.
1913. KURZ, A. Die Lochseen und ihre Umgebung. Archiv f. Hydrob. 8 p. 1.

1909. KUTTNER, O. Untersuchungen über Fortpflanzungsverhältnisse und Vererbung bei Cladoceren. Intern. Revue **2** p. 633—667.
1913. — Über Vererbung und Regeneration angeborener Miszbildungen bei Cladoceren. Archiv für Entwicklungsmechanik der Organismen **36** 4. H. p. 649.
1926. KYLE, H. M. The Biology of Fishes. London.
1838. LACORDAIRE, Th. Introduction à l'Entomologie **2** Paris.
1914. LANG, A. Die experimentelle Vererbungslehre in der Zoologie seit 1900 1^{ste} Hälfte. Jena.
- 1909a. LANGHANS, V. H. Über experimentelle Untersuchungen zu Fragen der Fortpflanzung, Variation und Vererbung bei Daphniden, Verhandl. d. Deutsch. Zool. Gesellschaft p. 281.
- 1909b. *— Planktonprobleme Lotos **57** p. 172.
1911. — Cladoceren aus dem Salzkammergut. *ibid.* 59.
1914. LANTSCH, K. Studien über das Nannoplankton des Zugersees und seine Beziehung zum Zooplankton. Zeitschr. f. wiss. Zool. **108** p. 631.
1900. LAUTERBORN, R. Der Formenkreis von *Anuræa cochlearis* I. Verh. d. Naturh.-Medic. Vereins zu Heidelberg. N. F. **6** p. 412.
- *ibid.* II N. F. **7** p. 529.
1912. LENZ, F. Ueber idioplasmatische Ursachen der physicalischen und pathologischen Sexualcharaktere der Menschen. Arch. f. Rass. u. Ges. Biol. **9** p. 545.
1900. LEVANDER, K. M. Zur Kenntnis des Lebens in den stehenden Kleingewässern auf den Skäreninseln. Acta soc. pro fauna et flora Fennica. Helsingfors **18** Nr. 6 p. 1.
1900. LILLJEBORG, W. *Cladocera Sueciæ*. Upsala.
1911. LIST, F. Beiträge zur Kenntniss des Planktons einiger Teiche in der Umgegend von Darmstadt. Zeitschrift für Fischerei **16** p. 1.
1917. — Das Teichplankton in der Umgegend von Darmstadt nach ununterbrochenen Beobachtungen in den Jahren 1908—1916. Zeitschrift für Fischerei **3** N. F. p. 1.
1920. — Das Plankton einiger Kolke des Altrheins bei Erfelden und ein Vergleich des Kolkplanktons mit dem einiger Teiche in der Umgegend von Darmstadt. Archiv für Hydrobiologie **12** p. 759.
1913. LITYŃSKI, A. Revision der Cladocerenfauna der Tatra-Seen. I. Teil. *Daphnidae*. Bulletin de l'Académie des Sciences de Cracovie. Série B p. 566.
- 1916a. — Litauische Cladoceren. Bulletin de l'Académie des Sciences de Cracovie. Octobre—Novembre—Décembre 1915 p. 248.
- 1916b. — Über den Bau der Extremitäten bei den Cladoceren und deren Bedeutung für das System. Bulletin de l'Académie des Sciences de Cracovie. Série B. Janvier—Février—Mars 1916 p. 3.
1912. *LLOYD, R. E. The growth of groups in the animal kingdom. London. After Turesson.
1909. LOHMANN, H. Die Gehäuse und Gallertblasen der Appendicularien. Verhdl. d. Deutschen Zool. Gesellsch. **19** p. 201.
1911. — Ueber das Nannoplankton und die Zentrifugierung kleinster Wasserproben zur Gewinnung desselben in lebendem Zustande. Intern. Revue **4** p. 1.
1916. LOTSY, J. P. Evolution by means of Hybridization. Hague.
1902. LOZERON, H. Sur la répartition verticale du plancton dans le lac de Zürich, de décembre 1900 à décembre 1901. Vierteljahrsschrift d. Naturf. Ges. Zürich **47** 1902 p. 1.
1905. LUTHER, A. D. Zur Kenntnis der Gattung *Macrostoma*. Festschr. f. Palmén. Vol. I **5**.
1903. MARSH, C. D. The plankton of Lake Winnebago and Green Lake. Wisconsin geological and natural history survey. Bulletin No. **12** p. 1.
1921. MEISENHEIMER, J. Geschlecht und Geschlechter im Tierreich. Jena.
1923. — Die Vererbungslehre. Jena.
1917. MINKIEWICZ, S. Die Crustaceen der Tatraseen. Eine physiographisch-faunistische Skizze. Bulletin de l'Académie des Sciences de Cracovie. Série B. Novembre—Décembre. 1916. p. 262.

1905. MURRAY, J. On the distribution of the pelagic organisms in Scottish lakes. Proceed. Royal. phys. Soc. Edinburgh **16** p. 51.
1911. — The annual history of a periodic pond. Internat. Revue **4** p. 300.
1868. MÜLLER, P. E. Danmarks *Cladocera*. Naturhist. Tidsskr. København 3. R. **5** p. 53.
1870. — Notes sur les Cladocères des grands lacs de la Suisse. Archives d. sci. phys. et natur. 2. pér. **37** p. 1.
1853. MÜLLER, H. Ueber das Männchen von *Argonauta argo* und die Hectocotylen. Zeitschr. f. wiss. Zool. **4** p. 1.
1914. NAUMANN, E. Beiträge zur Kenntnis des Teichnannoplanktons. Biologisches Centralblatt **34** No. 9 p. 581.
1918. — Ueber die natürliche Nahrung des limnischen Zooplanktons. Lunds Universitets Aarskrift. N. F. Avd. II Bd. 14 N. 31.
1921. — Specielle Untersuchungen über die Ernährungsbiologie des tierischen Limnoplanktons. I *ibid.* Bd. 17 Nr. 4.
1923. — *do.* II *ibid.* Bd. 19 N. 6.
1924. — Untersuchungen über einige gallertführende Tiere des Limnoplanktons. Archiv für Zoologi. Nr. 24.
1924. — Untersuchungen über das Verteilungsproblem des limnischen Biosestons II—III. *ibid.* Nr. 25 und 26.
1866. *NÄGELI, C. Ueber den Einfluss der äusseren Verhältnisse auf die Varietätenbildung im Pflanzenreiche. Botan. Mitteilungen **2** München.
1875. NEUMAYR, M. u. P. Die Congerien und Paludinenschichten Westslavoniens. Abh. geolog. Reichsanstalt Wien **7**.
1908. NORDQUIST, H. Sommaren 1907 i Aneboda Fiskeriförsöksstations Fiskdammar funna Cladocerer. Skrifter utgifna af södra Sveriges Fiskeriförening. Nr. 3 1908 p. 1.
1921. — Studien über das Teichzooplankton. Lunds Universitets Aarskrift. N. F. **17** Nr. 5 p. 1.
1910. NORDQUIST, O. Über das Eindringen des Lichtes in von Eis und Schnee bedeckten Seen. Internat. Revue **3** p. 79.
1918. OLUFSEN, O. Studien über die Süsswasserfauna Spitzbergens. Zoologiske Bidrag Upsala p. 183 1918.
1906. OSTENFELD, C. and WESENBERG-LUND, C. A regular fortnightly exploration of the plankton of the two Icelandic lakes Thingvallavatn and Myvatn. Proceed. Roy. Soc. Edinburgh **25** p. 1092.
1902. OSTWALD, W. Zur Theorie des Planktons. Biolog. Centralbl. **22** p. 596.
- 1903a. — Zur Theorie der Schwebvorgänge sowie der spezifische Gewichtsbestimmungen schwebender Organismen. Arch. f. die ges. Physiologie. Bonn **94** p. 251.
- 1903b. — Zur Theorie der Richtungsbewegung schwimmender niederer Organismen. *ibid.* **95** p. 23.
- 1903d. — Theoretische Planktonstudien. Zool. Jahrb. Abth.-Syst. **18** p. 1.
1904. — Experimentelle Untersuchungen über den Saisonpolymorphismus bei Daphniden. Archiv für Entwicklungsmechanik **18** Dissert. p. 3.
1910. PAPANICOLAU, G. Experimentelle Untersuchungen über die Fortpflanzungsverhältnisse der Daphniden (*Simocephalus vetulus* und *Moina rectirostris* var. *Lilljeborgii*). Biol. Centb. **30** p. 689, 737, 753, 785; **31** 81.
1911. — Experimentelle Untersuchungen über die Fortpflanzungsverhältnisse bei Daphniden. **32** p. 81.
1919. PAULY, M. Die Einwirkung von Minereraldüngung auf die planktonischen Lebewesen in Teichen. Zeitschrift für Fischerei **4** N. F. p. 210.
1920. — Zur Frühjahrswanderung der Uferfauna im grossen Müggelsee. Zeitschrift für Fischerei **3** N. F. p. 77.

1880. PAVESI, P. Une série de recherches sur la faune pélagique des lacs du Tessin et d'Italie. Arch. sc. phys. et nat. Genève Pér. **3** p. 151.
1911. PETRUNKEWITSCH, A. Sense of sight, courtship and mating in *Dugesia hentzi*. Zool. Jahrb. Syst. **31**.
1907. PLATE, L. Die Variabilität und die Artbildung nach dem Prinzip geographischer Formenketten bei den *Cerion* Landschnecken der Bahama Inseln. Archiv f. Rassen- und Gesellsch. Biol. **4** p. 581.
- 1913a. — Vererbungslehre. Leipzig.
- 1913b. — Selektionsprinzip und Problem der Artbildung. Leipzig und Berlin.
1916. PRASHAD, B. The seasonal conditions governing the pond life in the Punjab. Journal and Proceedings Asiatic Society of Bengal **12** p. 141.
1922. RABAUD, E. L'adaptation et l'évolution. Paris.
1926. RENSCH, B. Rassenkreisstudien bei Molusken I. Zoolog. Anzeiger **67** p. 253.
1919. REVERDIN, L. Étude phytoplantonique expérimentale et descriptive des Eaux du Lac de Genève. Archives des Sciences physiques et naturelles **1** p. 5.
1909. RIDGEWAY, W. Contributions to the Study of the *Equidæ*. Proceed. Zoolog. Society p. 547.
1921. ROBERT, H. Contribution à l'Étude du Zooplancton du lac de Neuchâtel. Bulletin de la Société neuchâteloise des sciences naturelles **45** p. 5.
1905. RUTTNER, F. Über das Verhalten der Oberflächenplanktons zu verschiedenen Tageszeiten im Groszen Plöner See und in zwei nordbömischen Teichen. Forschungsberichte Plön **12** p. 35.
1909. — Ueber tägliche Tiefenwanderungen von Planktontierchen unter dem Eise und ihre Abhängigkeit vom Lichte. Intern. Revue **2** p. 397.
- 1914a. — Bemerkungen zur Frage der vertikalen Planktonwanderung. Intern. Revue p. 1.
- 1914b. — Uferflucht des Planktons und ihr Einfluss auf die Ernährung der Salmonidenbrut. ibid. Biol. Suppl. **6** p. 1.
- 1914c. — Die Verteilung des Planktons in Süßwasserseen. Abderhalden: Fortschritte der Naturw. Forschung **10** p. 273.
1912. RÜHE, F. E. Monographie des Genus *Bosmina*. Zoologica **25** p. 1.
1913. — Biologie und Verbreitung der *Bosminen* und deren Beziehungen zur Eiszeit. Intern. Rev. p. 77.
- 1898—1899. SARASSIN, P. & F. Materialien zur Naturgeschichte der Insel Celebes. Vol. I—Vol. II.
1890. SARS, G. O. Oversigt af Norges Crustacea II. *Branchiopoda, Ostracoda, Cirripedia*. Videnskabselsk. Forh. p. 1.
1916. SCHÄDEL, A. Produzenten und Konsumenten im Teichplankton. Archiv f. Hydrob. u. Planktonk. **11** p. 404.
1763. SCHAEFFER, J. C. Die grünen Armpolypen. Die geschwänzten und ungeschwänzten zackigen Wasserflöhe. Regensburg.
1910. SCHARFFENBERG, W. v. Studien und Experimente über die Eibildung und den Generationszyklus von *Daphnia magna*. Intern. Revue Biol. Suppl. I p. 42.
1914. — Weitere Untersuchungen an Cladoceren über die experimentelle Beeinflussung des Geschlechts und der Dauereibildung. Intern. Revue Biol. Suppl. **6** p. 1.
1908. SCHEFFELT, E. Die Copepoden und Cladoceren des südlichen Schwarzwaldes. Archiv für Hydrobiologie und Planktonkunde **4** p. 91.
1905. SCHMIDTMANN: Handbuch der gerichtlichen Medizin p. 193.
1913. SCHNEIDER, G. Das Plankton der westfälischen Talsperren des Sauerlandes. Archiv f. Hydrobiologie und Planktonkunde **8** p. 1, 207.
1904. SCHRÖDER, CHR. Kritische Beiträge zur Mutations, Selektions, und zur Theorie der Zeichnungsphylogenie bei den Lepidopteren. Allgem. Zeitschr. f. Entom. **9**.

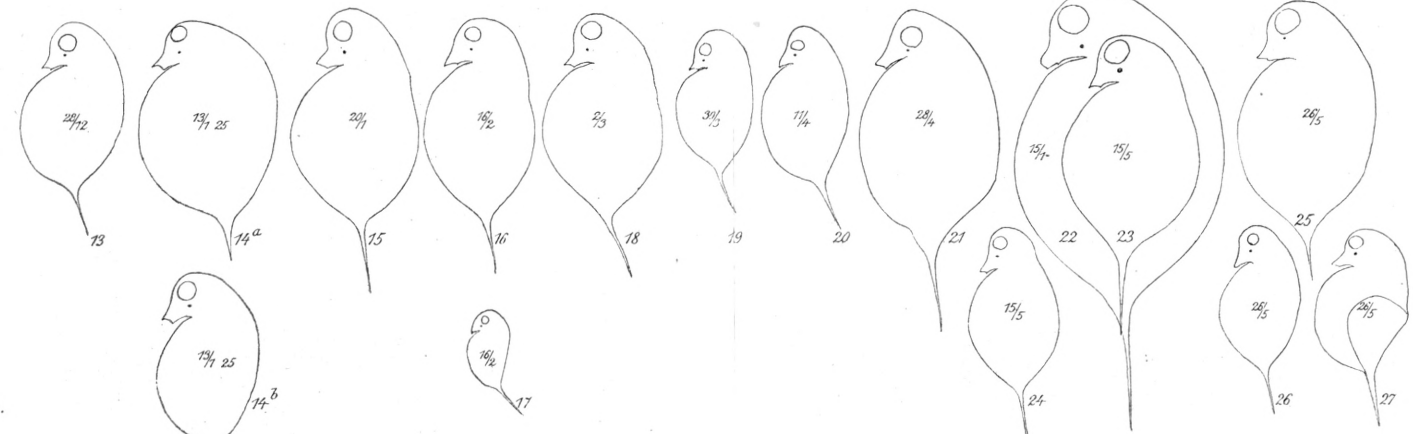
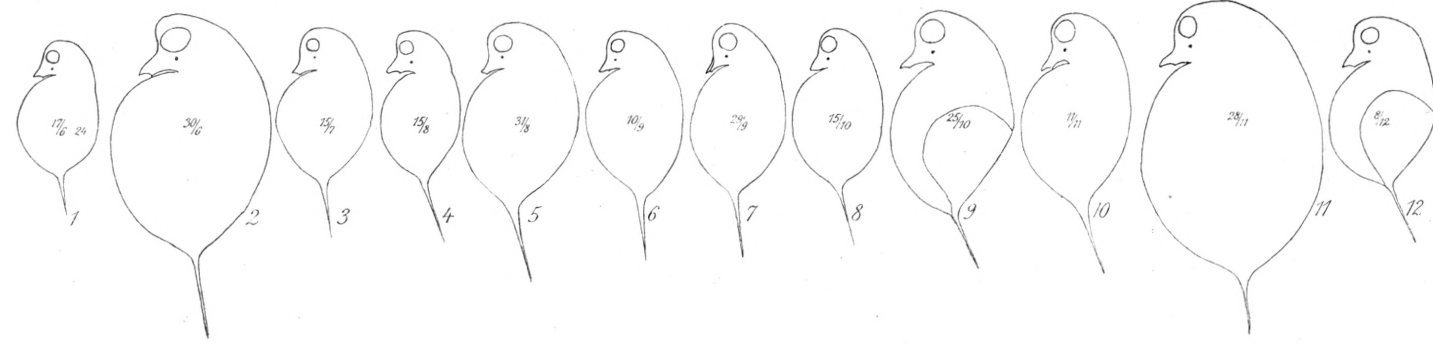
1901. SCHRÖTER, C. und VÖGLER, P. Variationsstatistische Untersuchung über *Fragilaria crotonensis* (Edw.) Kitton im Plankton des Zürichsees in den Jahren 1896—1901. Vierteljahrschr. d. Naturf. Ges. Zürich **46** p. 185.
1896. SCOURFIELD, D. J. The Entomostraca and the surface film of water. Journ. Linnean Soc. Zool. **25** p. 1.
1900. — The swimming peculiarities of *Daphnia* and its allies. Journ. Quekett Micr. Club. London Ser. II **7** p. 309.
1912. SEMON, R. Das Problem der Vererbung "erworbener Eigenschaften". Leipzig.
1894. STANDFUSZ, M. Über die Gründe der Variation und Aberration des Falterstadiums bei den Schmetterlingen. Insektenbörse. **11**.
1895. — Weitere Mitteilungen über den Einfluß extremer Temperaturen auf Schmetterlingspuppen. Entom. Zeit.
- 1899.* — Gesamtbild der bis Ende 1898 an *Lepidoptera* vorgenommenen Temperatur- und Hybridationsexperimente. Insektenbörse **16**.
1905. — Die Resultate 30-jähriger Exper. mit Bezug auf Artbildung und Umgestaltung in Tierwelt. Verh. Schweizer. naturf. Ges. Luzern.
1913. STEINER, H. Das Plankton und die makrophytische Uferflora des Luganersees. Intern. Revue. Biol. Suppl. VI Ser.
1907. STEINMANN, G. Die Tierwelt der Gebirgsbäche. Brüssel.
1894. STINGELIN, TH. Ueber zwei neue Daphniden aus dem schweizerischen Hochgebirge. Zool. Anz. **17** p. 378.
1895. — Die Cladoceren in der Umgebung von Basel. Rev. Suisse de Zool. Genève **3** p. 161.
1897. — Ueber jahreszeitliche, individuelle und lokale Variation bei Crustaceen. Forschungsber. Plön **5** p. 150.
1906. — Neue Beiträge zur Kenntnis der Cladocerenfauna der Schweiz. Revue suisse de Zoologie **14** p. 317.
1910. — Crustaceen aus kleineren Seen der Unterwaldner- und Berneralpen. Revue suisse de Zoologie **18** p. 105.
1917. SUCHLAND, O. Beobachtungen über das Phytoplankton des Davoser Sees. Dissert. Davos.
1910. THALLWITZ, J. Beobachtungen über den Saisonpolymorphismus einiger Planktoncladoceren. Jahresbericht der Annenschule Dresden-Altstadt. Nr. 765 p. 5.
1905. THIENEMANN, A. Biologie der Trichopteren-Puppe. Dissert.
1914. — R. Wolterecks Arbeit über Funktion, Herkunft und Entstehungsursachen der sogen. Schwebe-Fortsätze pelagischer Cladoceren. Arch. f. Hydrob. u. Planktonk. **9** p. 656.
1906. TOWER, W. L. An Investigation of Evolution in Chrysomelid Beetles of the Genus *Leptinotarsa*. Carnegie Institution of Washington. Publ. 48.
1913. v. TRANSEHE, N. Studien über Temperaturwirkungen auf *Daphnia magna* mit besonderer Berücksichtigung der Anpassungserscheinungen. Dissert. Leipzig.
1922. TURESSON, G. The genotypical response of the plant species to the habitat. Lund.
1912. WAGLER, E. Faunistische und biologische Studien an freischwimmenden Cladoceren Sachsens. Zoologica **67** p. 305.
1923. — Über die Systematik, die geographische Verbreitung und die Abhängigkeit der *Daphnia cucullata* Sars von physikalischen und chemischen Einflüssen des Millieus. Internat. Revue p. 41; 1924 p. 265.
1913. WAHLBERG, A. Bidrag till Kännedomen om Littois-Träsk med särskild Hänsyn till dess Plankton. Acta Societata pro Fauna et Flora Fennica **38** p. 5.
1915. WARMING, EUG. Nedstammingslæren. Udvalget for Folkeoplysningens Fremme. København.
1874. WEISMANN, A. Ueber Bau und Lebenserscheinungen von *Leptodora hyalina*. Zeit. f. wiss. Zool. **24** p. 1.

1879. WEISMANN, A. Beiträge zur Naturgeschichte der Daphnoiden. Zeitschr. wiss. Zool. **33** p. 55.
1902. — Vorträge über Descendenztheorie. Jena.
1909. WELDON, W. F. R. *Branchiopoda, Phyllopora* und *Cladocera* in Cambridge. Natural History **4** p. 18—52.
1894. WESENBERG-LUND, C. Grønlands Ferskvandsentomostraca I. *Phyllopora, branchiopoda* et *cladocera*. Vid. Med. Nat. Foren. København **56** p. 82.
1899. — Danmarks *Rotifera* I. Vid. Med. Nat. Foren. København **61** p. 1.
1900. — Von dem Abhängigkeitsverhältnis zwischen dem Bau der Planktonorganismen und dem spezifischen Gewicht des Süßwassers. Biolog. Centralbl. **20** p. 606 u. 644.
1906. see Ostenfeld and Wesenberg-Lund.
- 1904—1908. — Planktoninvestigations of the Danish lakes. København.
- 1908a. — Die littoralen Tiergesellschaften unserer grösseren Seen. Intern. Revue **1** p. 574.
- 1908b. — *Culex-Mochlonyx-Corethra*, eine Anpassungsreihe. Intern. Revue **1** p. 513.
1910. — Grundzüge der Biologie und Geographie des Süßwasserplanctons. Intern. Revue **3** Biol. Supp. 1.
1913. — Odonaten-Studien. Intern. Revue p. 155—228; p. 373—422.
1922. — Contributions to the Biology of Danish *Amphibia* **10** p. 23—30; 209—232; 321—361.
1905. VOIGT, M. Die vertikale Verteilung des Planktons im Grossen Plöner See und ihre Beziehungen zum Gasgehalt dieses Gewässers. Plöner Forschungsberichte **12** p. 115.
1912. WOLOSZYNSKA, J. Das Phytoplankton einiger javanischen Seen mit Berücksichtigung des Sawa-Plankton. Bulletin de l'Académie des Sciences de Cracovie p. 649.
1912. VOLLMER, C. Über die Entwicklung der Dauereier der Cladoceren. Biologisches Centralblatt **32** p. 119.
- 1908a. WOLTERECK, R. Über natürliche und künstliche Varietätenbildung bei Daphiden. Verhandl. d. Deutsch. Zool. Gesellschaft. 1908. p. 234.
- 1908b. — Die natürliche Nahrung pelagischer Cladoceren. Intern. Revue I p. 871.
1909. — Weitere experimentelle Untersuchungen über Artveränderung, speziell über das Wesen quantitativer Artunterschiede bei Daphniden. Verh. deutsch. Zool. Gesellsch. **19** p. 110.
- 1911a. — Ueber Veränderung der Sexualität bei Daphniden. Intern. Rev. **4** p. 91.
- 1911b. — Beitrag zur Analyse der "Vererbung erworbener Eigenschaften". Transmutation und Präinduktion bei Daphnia. Verhandlung der Deutschen Zoologischen Gesellschaft 1911. p. 142.
1913. — Ueber Funktion, Herkunft und Entstehungsursachen der sogen. "Schwebefortsätze" pelagischer Cladoceren. Zoologica **67** p. 475.
1919. — Variation und Artbildung I. Bern 1919.
1919. WUNDSCH, H. H. Studien über die Entwicklung der Ufer- und Bodenfauna. Zeitschrift für Fischerei **4** N. F. p. 408.
1920. — Beiträge zur Frage nach dem Einfluss von Temperatur und Ernährung auf die quantitative Entwicklung von Süßwasserorganismen. Zoologische Jahrbücher **38** p. 1. Abt. f. allg. Zool. u. Physiol.
1893. ZACHARIAS, E. Faunistische und biologische Beobachtungen am Gr. Plöner See. Forschungsber. Plön **1** p. 27.
- ZELINKA, C. Die Rotatorien der Plankton-Expedition. Ergebnisse der Plankton-Expedition der Humboldt Stiftung **2** H. A.
1900. ZSCHOKKE, F. Die Tierwelt der Hochgebirgseen. Denkschr. d. Schweiz. naturf. Gesell. Zürich **37** p. 1.

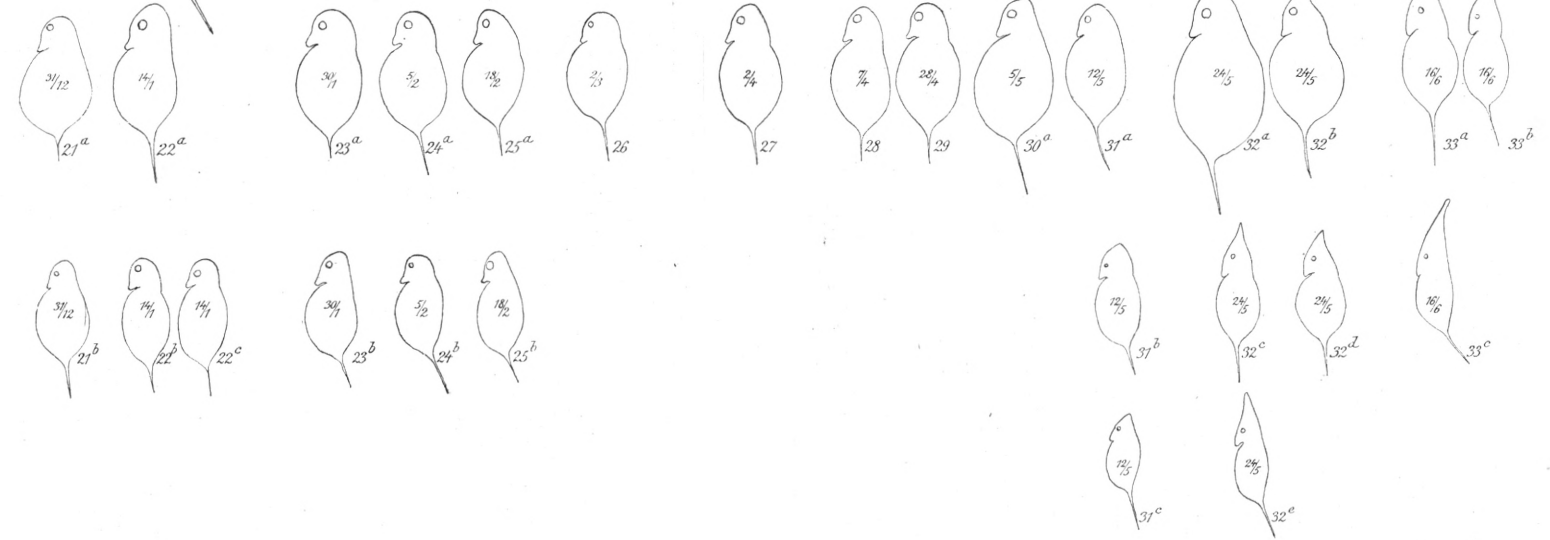
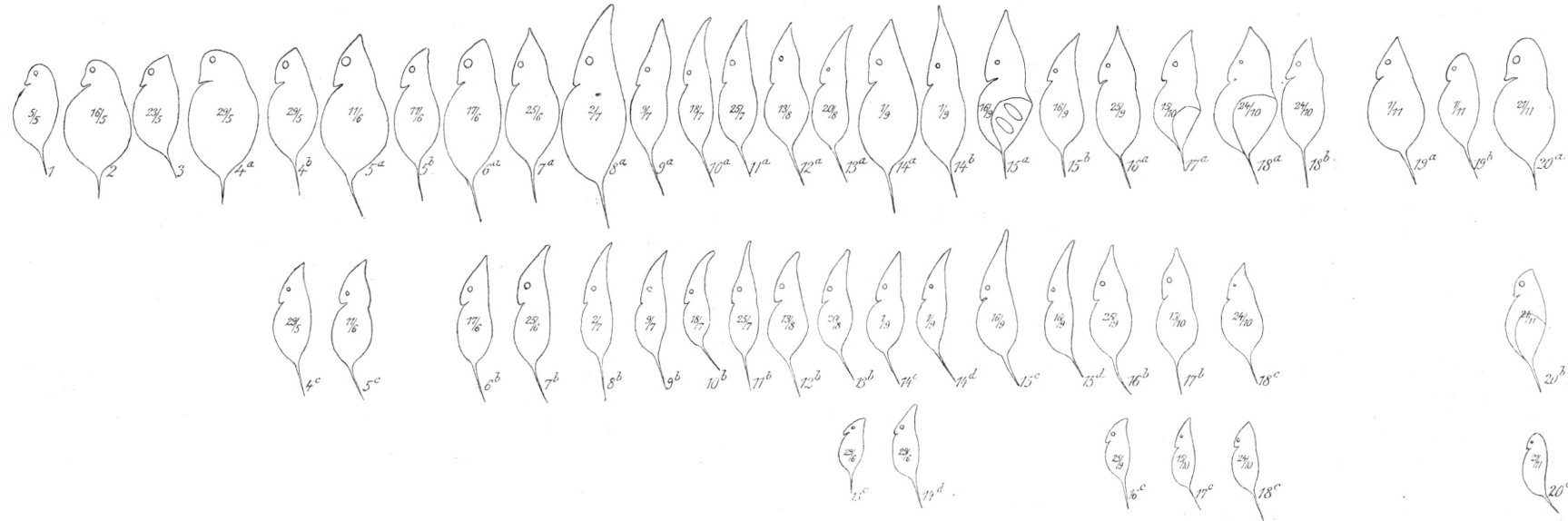
CONTENTS

	Pag.
Introduction	91— 95
Special part	95—146
<i>Daphnia magna</i>	95— 99
— <i>pulex</i>	99—109
— <i>longispina</i>	109—126
— <i>cucullata</i>	126—146
Theoretical remarks	146—200
Remarks of heredity	200—242
List of Literature	243—250

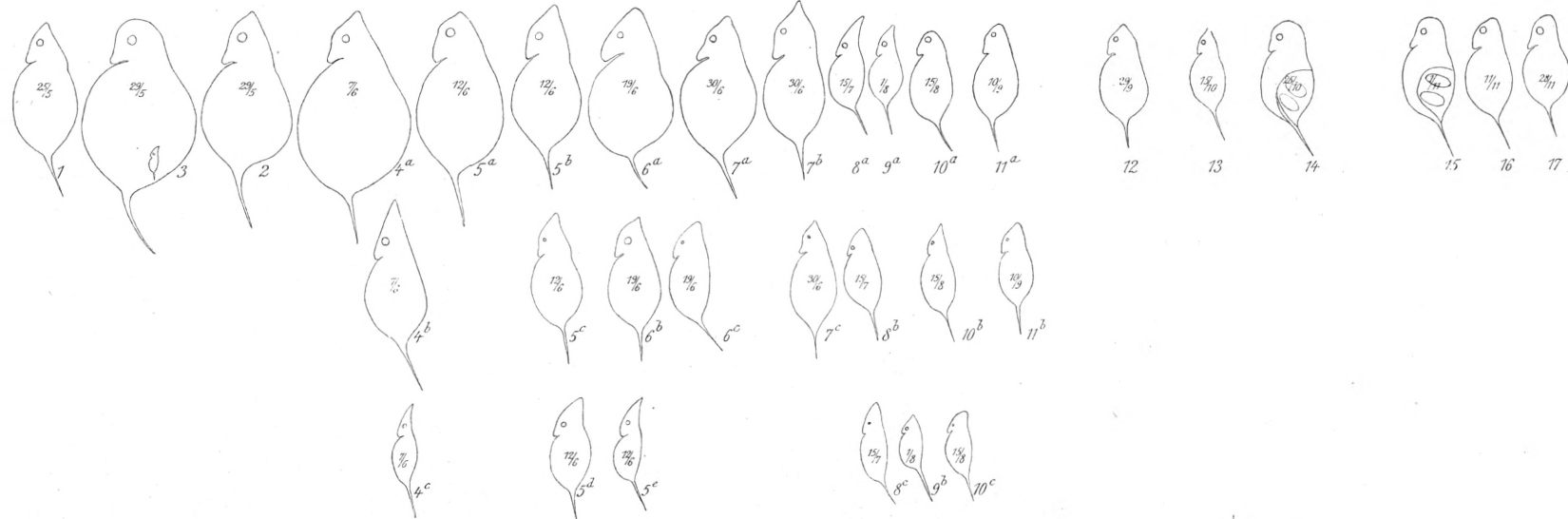
D. longispina. Hestekopond.



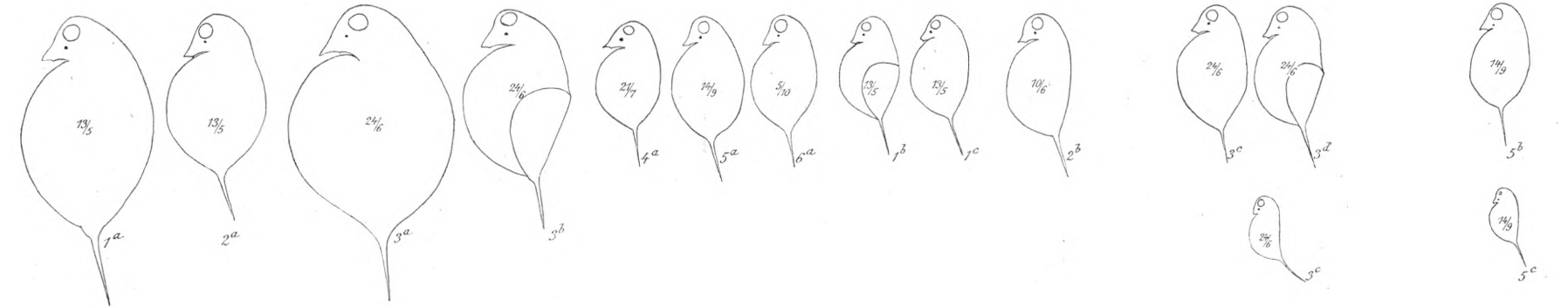
D. cucullata. Frederiksborg castle lake.



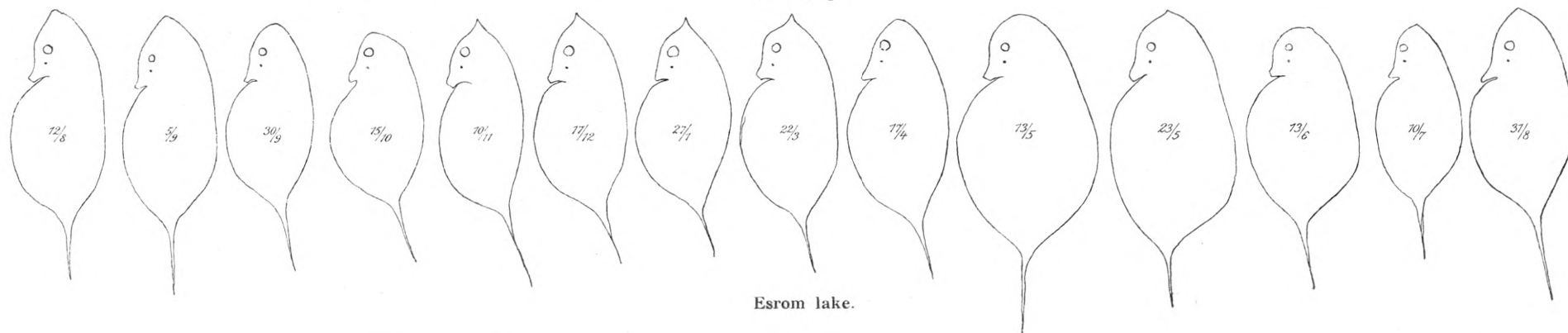
D. cucullata. Hestekopond.



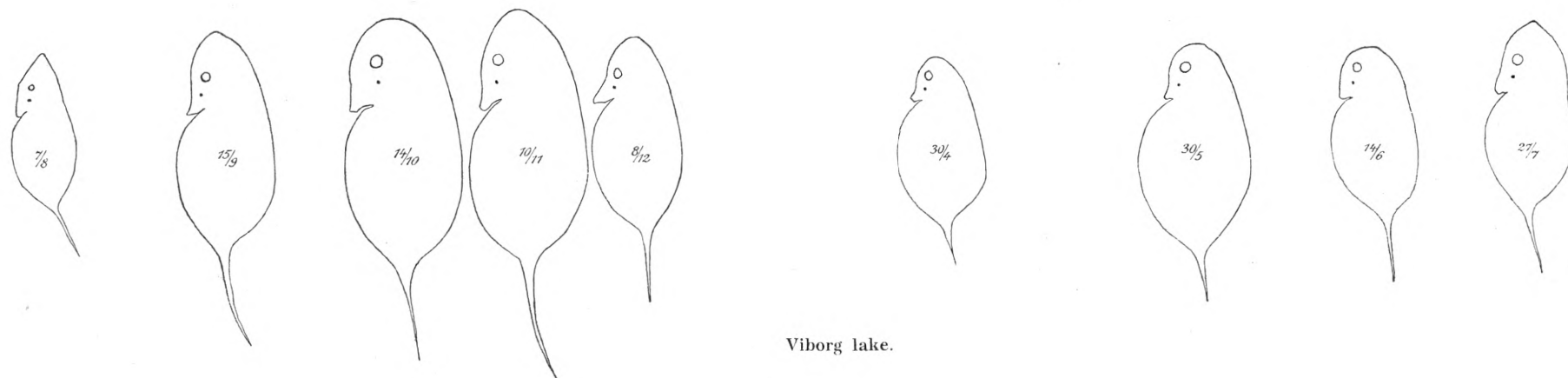
D. longispina. Klare lake.



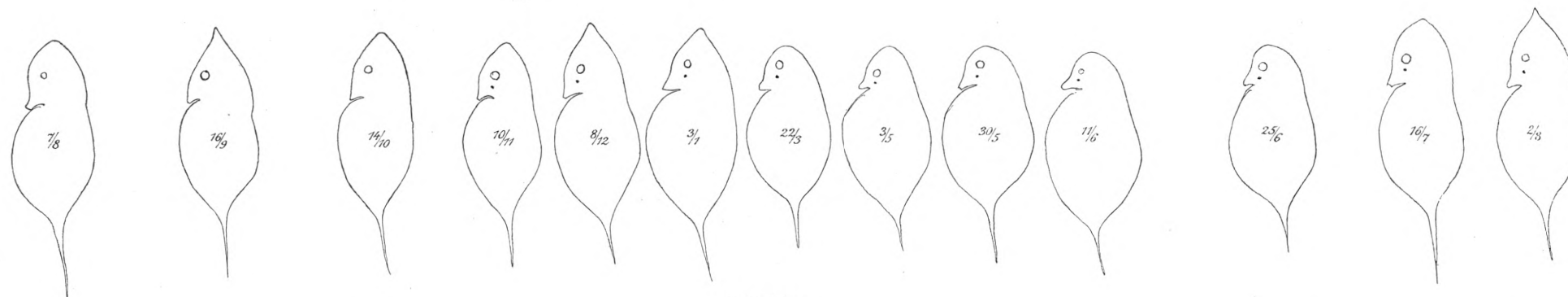
D. longispina.



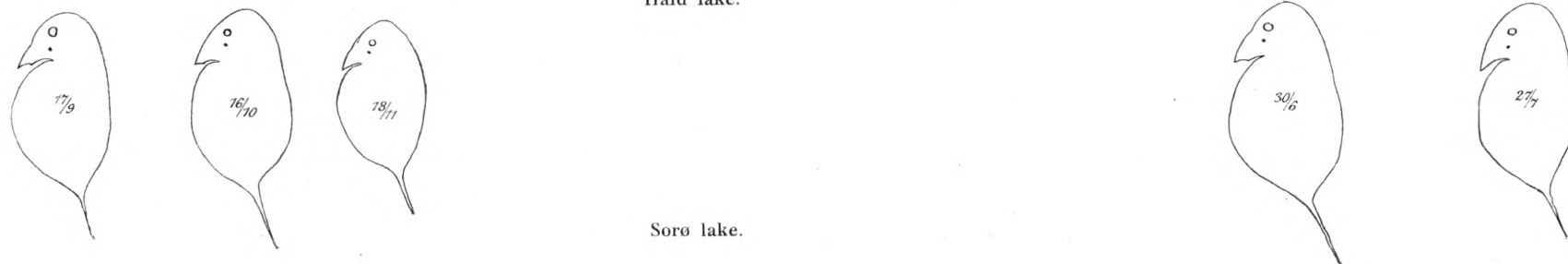
Esrom lake.



Viborg lake.



Hald lake.



Sorø lake.

CORRIGENDA

p. 165, l. 23. scool: read school

p. 199, l. 5 fr. b. Nevertheless, in some series of papers:
read Nevertheless, in some papers

p. 216, l. 15 fr. b. as in February at twelve with the: read
as in October, at twelve with a

p. 216, note. G.: read K.

p. 231, l. 11. species: read spaces

p. 242, l. 13. idiopinetic: read idiocinetic.

Det Kgl. Danske Videnskabernes Selskabs Skrifter.
 Naturvidenskabelig og matematisk Afdeling,
 8de Række.

	Kr. Øre
I, 1915—1917	10. 75.
1. Prytz, K. og J. N. Nielsen: Undersøgelser til Fremstilling af Normaler i Metersystemet, grundet paa Sammenligning med de danske Rigsprototyper for Kilogrammet og Meteren. 1915.....	1. 55.
2. Rasmussen, Hans Baggsgaard: Om Bestemmelse af Nikotin i Tobak og Tobaksextrakter. En kritisk Undersøgelse. 1916	1. 75.
3. Christiansen, M.: Bakterier af Tyfus-Coligruppen, forekommende i Tarmen hos sunde Spædkalve og ved disses Tarminfektioner. Sammenlignende Undersøgelser. 1916	2. 25.
4. Juel, C.: Die elementare Ringfläche vierter Ordnung. 1916	» 60.
5. Zeuthen, H. G.: Hvorledes Mathematiken i Tiden fra Platon til Euklid blev en rationel Videnskab. Avec un résumé en français. 1917.....	8. 00.
II, med 4 Tavler, 1916—1918	11. 50.
1. Jørgensen, S. M.: Det kemiske Syrebegrebs Udviklingshistorie indtil 1830. Efterladt Manuskript, udgivet af <i>Ove Jørgensen og S. P. L. Sørensen</i> . 1916	3. 45.
2. Hansen-Ostenfeld, Carl: De danske Farvandes Plankton i Aarene 1898—1901. Phytoplankton og Protozoer. 2. Protozoer; Organismer med usikker Stilling; Parasiter i Phytoplanktoner. Med 4 Figurgrupper og 7 Tabeller i Teksten. Avec un résumé en français. 1916	2. 75.
3. Jensen, J. L. W. V.: Undersøgelser over en Klasse fundamentale Uligheder i de analytiske Funktioners Theori. I. 1916.....	» 90.
4. Pedersen, P. O.: Om Poulsen-Buen og dens Teori. En Experimentalundersøgelse. Med 4 Tavler. 1917	2. 90.
5. Juel, C.: Die gewundenen Kurven vom Maximalindex auf einer Regelfläche zweiter Ordnung. 1917	» 75.
6. Warming, Eug.: Om Jordudløbere. With a Résumé in English. 1918	3. 65.
III, med 14 Kort og 12 Tavler, 1917—1919	26. 00.
1. Wesenberg-Lund, C.: Furesøstudier. En bathymetrisk Undersøgelse af Mølleaaens Søer. Under Medvirkning af Oberst <i>M. J. Sand</i> , Mag. <i>J. Boye Petersen</i> , Fru <i>A. Seidelin Raunkjær</i> og Mag. sc. <i>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. Lehmann, Alfr.: Stofskifte ved sjælelig Virksomhed. With a Résumé in English. 1918	3. 15.
3. Kramers, H. A.: 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.
IV, med 15 Tavler og 1 Kort	28. 50.
1. Bohr, N.: On the Quantum Theory of Line-Spectra. Part I. 1918	2. 25.
— Samme. Part. II. 1918.....	4. 00.
— — — III. 1922.....	1. 25.
2. Warming, Eug.: Økologiens Grundformer. Udkast til en systematisk Ordning. 1923	4. 50.
3. Wesenberg-Lund, C.: Contributions to the Biology of the Danish Rotifera. With 15 Plates and 18 Textfigures. 1923.....	21. 25.
4. Hertzprung, Ejnar: Effective Wavelengths of Stars in the Pleiades from plates taken at Mount Wilson. With 4 Figures and 1 Map. 1923.....	4. 75.

	Kr. Øre
V , med 57 Tavler	46. 90.
1. Bjerrum, Niels und Kirschner, Aage : Die Rhodanide des Goldes und das freie Rhodan. Mit einem Anhang über das Goldchlorid. 1918.....	3. 50.
2. Orla-Jensen, S. : The lactic acid Bacteria. With 51 Plates. 1919	46. 00.
3. Brünnich Nielsen, K. : Zoantharia from Senone and Paleocene Deposits in Denmark and Skaane. With 4 Plates. 1922	5. 25.
4. Petersen, Axel : Bidrag til de danske Simuliers Naturhistorie. Med 2 Tavler, 53 Figurer og 1 Kort i Texten. 1924.....	7. 75.
VI , med 12 Tavler	25. 70.
1. Christensen, Carl : A Monograph of the genus Dryopteris. Part II. 1920	8. 25.
2. Lundblad, O. : Süßwasseracarinen aus Dänemark. Mit 12 Tafeln und 34 Figuren im Text. 1920.	18. 50.
3. Børgesen, F. : 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.
VII , med 29 Tavler.....	37. 50.
1. Wesenberg-Lund, C. : Contributions to the Biology of the Danish Culicidæ. With 21 Plates and 19 Figures in the text. 1920—21	29. 00.
2. Nørlund, N. E. : Stirlings Interpolationsrække. 1924	4. 50.
3. Levinsen, G. M. R. : 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.
VIII.	
Jessen, Knud og Jens Lind : Det danske Markkruddts Historie. Med 1 Oversigtsskema. 1922—23.	24. 50.
IX , med 5 Tavler.	
Thoroddsen, Th. : Die Geschichte der isländischen Vulkane (nach einem hinterlassenen Manuskript). Mit 5 Tafeln. 1925.....	25. 15.
X , med 30 Tavler og 2 Kort	38. 10.
1. Wesenberg-Lund, C. : Contributions to the Biology of Zoothamnium Genuculatum Ayrton. With 14 Plates. 1925.....	14. 00.
2. Micoletzky, H. : Die freilebenden Süßwasser- und Moornematoden Dänemarks nebst Anhang über Amöbosporidien und andere Parasiten bei freilebenden Nematoden. Mit 13 Tafeln und einer Textfigur sowie mehreren Tabellen. 1925	25. 75.
3. Gram, J. P. : Tafeln für die Riemannsche Zetafunktion. Herausgegeben von N. E. Nørlund. 1925	1. 00.
4. Johs. Schmidt : 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.
5. Jul. Hartmann : A Comparison between the Flow of Water and Mercury in Pipes with a view to testing the Osborne Reynolds' Law of Similarity. With 3 Plates and 18 Figures in the text. 1926	5. 00.
XI.	
1. Luplau Janssen, C. : La Surface de la Planète Jupiter 1919—1924. Avec 7 planches. 1926.....	10. 00.
2. Wesenberg-Lund, C. : Contributions to the Biology and Morphology of the Genus Daphnia with some Remarks on Heredity. With 2 Plates and 21 Textfigures. 1926.....	13. 20.