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Abstract of thesis for Ph.D.

A study of the Physiology and Ecology of certain Cladocera

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Comparatively little work has been done on the ecology of Cladocera except in regard to planktonic varieties , and special subjects such as cyclomorphosis .

This thesis is an attempt to ascertain the factors governing the occurence and distribution of Cladocera , by means of a special , mainly laboratory , study of certain factors combined with a general field-survey .

Temperature , the factors influencing parthenogenetic reproduction , and food-supply were specially studied .

It was not possible , except for a few varieties , to correlate resistance to high temperatures with occurence and distribution. Resistance to low temperatures was correlated with seasonal but not with spatial occurence .

The effects of temperature , crowding , amount of food , and light on parthenogenetic reproduction were investigated . Increased temperatures increase frequency of moulting , and shorten the duration of the pre-adult phase . Egg-number may or may not be reduced , the behaviour being probably associated with the seasonal occurenece of the species . The other factors all have marked effects on egg-number , varying somewhat as between species . They have no effect on frequency of moulting or logevity . Food and temperature effects show no inter-action .

A general survey was made of the distribution of Cladocera in lakes and pools in Scotland , England , and Denmark . Notes were made on individual species . The opportunity was taken of clearing up some taxonomic difficulties .

Within habitats Cladocera often show marked localization . Factors responsible for this include :- food-supply ; presence and nature of vegetaion ; water-movement ; and type of bottom .

It is more difficult to correlate Cladoceran distribution with the general nature of the habitat . Most,but not all , Cladocera appear to be indifferent to trophicity and pH . Larger habitats have more varied faunas , and also somewhat acid habitats . General stability of the habitat is probably important .

Parasites are often fatal but are tooo rare to be important . Epibiotes are usually harmless . Many species prey on Cladocera , but only fish and tadpoles certainly control their numbers . Competition is probably very important in determining distribution , but related species often occur together .

Apaper on *Daphnia* systematics (in Ms. form) is included with this thesis .

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' A Study of the Physiology and Ecology of certain Cladocera '

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Table of contents .

Included with thesis , separately numbered :-

' The British Species of the Genus Daphnia ' Ms. copy .

A Study of the Physiology and Ecology of Certain Cladocera.

The Cladocera as a group have attracted great interest ever since the invention of the microscope. The earliest studies were, as to be expected, mainly morphological & systematical. Owing to the intensive studies of such workers as O.F. Müller (1785), Jurine (1820), G.O. Sars (many papers 1860-1920), P.E. Müller (1867), & Lilljeborg (1900 etc.), the main outlines of the systematics and general distribution of the group were known by the beginning of this century, at least as far as European species are ~~were~~ concerned, though much work still remains to be done on the details. This early period of 'discovery' was brought to an end by the publication of Lilljeborg's Cladocera Sueciae in 1900.

The published work since this period is immense, but, except in regard to a small number of species, and to certain special problems (mentioned below), it has added comparatively little to our knowledge.

Most attention has been paid to the problem of sexual reproduction, and the possibly related problem of cyclomorphosis. These have occupied a great number of workers of the highest calibre, from Weis~~s~~mann (1874-1880) to the present day. Outstanding are the contributions of Woltereck (1928, 1933 etc.), Wesenberg-Lund (1926 etc.), Berg (1931, 1933,) Mortimer (1935, 1936), Coker (1939) and Banta and his co-workers (1939 etc.). Neither problem can be considered to be fully elucidated, but a number of observations of general interest have been incidentally noted. Such of these as have a bearing on my research will be referred to at the appropriate places.

Largely in connection with these problems a certain amount of attention has been paid to the vertical distribution and migrations of planktonic Cladocera. Woltereck (1927) refers to a number of such investigations. Of great importance are those of Birge (1897), of Wesenberg-Lund (1904-1918), of Southern & Gardiner (1926), and of Lantzsch (1914), but there have been many others. Many attempts have been made to correlate the distribution of planktonic Cladocera with the trophic condition of lakes. For the most part these have been unsuccessful, and many authors such as Gurney (1923) have honestly admitted that there appears to be no correlation. More successful have been the studies of the ecological requirements of individual plankton species, such as those of Thienemann (1926) on Holopedium gibberum, and Rylov (1941) on Daphnia cristata. Where these affect species that I have dealt with, they will be referred to below.

A considerable number of investigators, such as Cannon (1933), Storch (1922, 1924), Eriksson (1934), Stuart and co-workers (1931 etc.), Naumann (many papers 1912 -), Woltereck (1928 etc.) and Lefèvre (1942) have investigated feeding mechanisms and food. Their work will be mentioned in more detail later. All that I need say here is that in very many points authors are in violent disagreement. This is particularly so in regard to the nature of the principal food of the Cladocera.

Other factors of ecological significance have been less studied. A certain amount of work has been done on thermal resistance, particularly by Brown (1929), and Brown and Crozier (1927). Pratt (1943) studied population development at various temperatures, and MacArthur and Baillie

(1929) have studied longevity and development in relation to temperature. There are a considerable number of casual observations and theoretical statements in the literature. However the role of temperature in the biology and ecology of Cladocera is by no means clearly understood.

A rather considerable number of workers, such as Harnisch (1925, 1929), Hubault (1933), Poulsen (1928), and Pacaud (1939), have studied the relations of various Cladocera to pH., calcium content of waters, and related factors. Except in regard to the so-called 'sphagnophile' forms, their works show comparatively little agreement. Other factors that have been studied are ; the effects of low oxygen tensions, by Fox (1948), Fox, Hardcastle and Dresel (1949), Pacaud (1939) etc., the effects of magnesium and zinc, Hutchinson (1933), the effect of osmotic pressures, Naumann (1933, 1934 etc.,) Krogh (1939) etc., and the effect of light, Schultz (1928-).

Various circumstances have tended to lessen the value of much of the previous work. Unavoidable was the effect of the chaotic state of the systematics of many genera and particularly of the much-used genus Daphnia. It is often quite impossible to be sure exactly which form a worker has been experimenting with. Two unfortunate tendencies are found in most fields of Cladoceran research; a proclivity to extend the results obtained for one species, or even one strain, to cover the whole of the group; and a tendency on the part of many authors to express results in the light of preconceived hypotheses, often resulting in the suppression or minimization of facts which do not accord with these. Further confusion has resulted from the failure of many authors to take sufficient account of the physiological variability of the species.

Thus the amound of assured knowledge which we possess is very much less than the quantity of published literature would indicate.

In recent years the Cladocera, particularly members of the genus Daphnia, have been much used as experimental animals in the investigation of various biological problems. Thus they have been used in studies of population development (Pratt 1943), ~~in the investigation of the synthesis and function of haemoglobin (Foxetal 1948, 1949, 1950 etc.)~~, and in the investigation of the effects of various drugs and poisons (Holm-Jensen 1944, Anderson 1945 etc.) The Cladocera are also of some economic importance, since they form a portion of the food of many fish.

In view of these facts it seemed to me that a rather thorough study of the ecology, and the relevant aspects of the physiology of the Cladocera would be of considerable use. It is not possible for one man to cover so wide a field in three years, so that a selection had to be made of subjects for investigation. I finally decided to combine an intensive, largely laboratory, study of certain factors as temperature and food, with a more general ecological survey, based mainly on numerous field collections. For convenience, I am treating these various aspects of my work separately.

Methods.

Little need be said about methods in this introduction, as few procedures were common to all aspects of the work.

Whenever living animals were to be examined this was done by enclosing them in a compressorium under just sufficient pressure to restrict movement without damaging the individual. For routine purposes an ordinary microscope was used, but whenever I required to see fine details I used a Cooke-Troughton monocular-binocular research microscope.

In all experimental work care was taken to ensure that the animals used were a fair sample of the population investigated. When an individual had been used for any experimental purpose whatsoever, it was immediately discarded and neither it nor its descendents were used again in any experiment.

Systematics and nomenclature.

The correct identification and naming of species is essential in any ecological work. In the Cladocera, as in many other invertebrate groups this is rendered more difficult by the confusion in which the systematics of the genus is involved. For identifications of species I have consulted most of the standard systematical works and especially Scourfield and Harding's key (1941), Richard's 'Revision des Cladocères,' (1895, 1896), Birge, 'The Water-fleas' in Ward and Whipple's 'Freshwater Biology' (1918), and Rylov's account in 'Die Binnengewasser' Band XV (1935). Wherever necessary I have checked my identifications against original descriptions and accounts given in special systematical works.

Though I have in general followed Scourfield and Harding (1941) in the main outlines of classification and nomenclature, I have not accepted their system in its entirety, since it is imperfect in some respects. The same criticism can be applied to all/published accounts known to me. The system I have finally derived expresses as accurately as possible the present state of our knowledge. I have taken care in all cases to ensure that even if our ideas of classification and nomenclature should change considerably in the future, the exact identity of the species with which I have worked will still be clear. In order to do this I have been forced in some cases to introduce considerable taxonomic and nomenclatorial changes, and also to provide short descriptions of some of the forms with which I have been concerned. In most genera I have included these systematical and morphological notes along with ecological notes on the respective species in the general part of this thesis (see below). For the genus Daphnia I had to make such considerable changes to the accepted classifications to be in conformity with recent published work and with my own observations, that I decided to publish these as a separate paper, now in the press. A manuscript copy of this paper is included with this thesis.

Terminology.

One of the major difficulties confronting the writer of an ecological paper is the lack of a standardized terminology in many spheres of his work. Unless a new term were to be invented to cover every slightly different ecological situation this could not be avoided. In most cases I prefer to adopt current terms and provide a definition of my usage. Where such terms are only used in one section of this thesis I shall define them on the occasion in which I first use them. Certain terms which I use constantly are best defined here.

The terms pond, pool and lake have been very variously used in limnological literature, and several attempts have been made to provide precise definitions; but all these are to some extent unsatisfactory, and none has won general acceptance. There is a tendency on the part of certain biologists to use pool only in the sense of a small pond. Whilst this appears to be correct American usage, it is very incorrect English usage. The Oxford Pocket Dictionary defines pond as a small body of still water, especially as made for watering cattle or other purposes. Pool is defined as

' A small body of water especially of natural formation, puddle, deep place in river.' This is more in accordance with normal English usage but the distinction between natural and artificial waters is so vague and so rarely adhered to in practise, that it is best ignored in scientific terminology. In my opinion the distinction between the terms pond and pool is more one of connotation and usage than of denotation. I shall, therefore, use these two terms interchangeably. Following the Oxford dictionary I use the term puddle to mean a small, dirty pool. The distinction between pools and lakes is clear enough in regard to typical examples. An ideal lake is a large body of water, deep enough to show thermal stratification in summer, with distinct littoral and limnetic zones, with discrete inflow and a definite outflow, and with some differentiation of the marginal vegetation depending on exposure to wave action. An ideal pool is a smaller body of water, not more than 1 to 3 metres deep and not showing thermal stratification to any marked extent, lacking distinct littoral and limnetic zones, gaining water solely by surface drainage and seepage, without a discrete outflow and with effects of wave-action negligible. Macan (1950 etc.), has introduced a third category for the Lake District of England, the tarn. This is defined as a smaller water-body than a lake, not lying in a principal drainage basin but with a ~~temporary~~ permanent outflow. This category cannot be usefully applied in ecological work based on results from a wide area. All the features mentioned above have at one time or another been used by some author as the distinction between pool and lake. Unfortunately adherence to any such system results in ridiculous assignments of natural waters, and so I have abandoned any such attempt. I have likewise found that classifications of habitats on biological grounds are impracticable. When I use the term lake in this thesis it merely means that the water-body in question has more in common with an ideal lake, in the sum-total of its characters, than it has with an ideal pool. Mutatis mutandis the same applies to my usage of the term pool. When used generally I intend the term lake to cover also artificial bodies of water of lake like character, i.e. reservoirs. The term lacustrine is used to imply animals or features characteristic of lakes, and to a lesser extent large ponds.

I have used the terms lenitic and lotic in their generally accepted sense, but have introduced the term sub-lenitic to cover a class of habitats in some respects intermediate between lenitic and lotic habitats, which are further discussed in the general portion of this thesis.

I have used the term locality to indicate definite area or water-body. The term station is used for a well-defined small portion of a locality in which I have collected. The term habitat is used primarily to cover a well-defined portion of a locality or station, distinguished by a definite combination of features of ecological importance, but also in a more general sense to cover such regions of all localities.

The various terms for frequency and abundance are often confused in the literature. In this thesis widely-distributed and localized are used in the sense of geographical range. The terms common, frequent, and rare, are used as a series to indicate how ~~often~~ frequently in time or space a form is found in a given area, habitat, or population. Abundant, numerous, and scarce are used to denote the relative numbers of individuals in a definite locality, station, or habitat at any one time.

Acknowledgements and responsibility.

Except where otherwise indicated I am solely responsible for the conceptions, facts and hypothesis contained in this thesis. Nevertheless many people have assisted me in various ways. Professor Fox has always been willing to discuss with me and criticize my views. He has gone to much trouble to obtain for me papers in obscure journals, necessary apparatus, and other research facilities. He has kindly placed at my disposal such records as he possessed of Cladoceran distribution, including the exact locality for his Apus pool in Hampshire. I am indepted to other members of this department also for stimulating discussions and criticisms. Miss G. Phear assisted me by maintaining my cultures and making collections whilst I was in Denmark and by determining the oxygen content of my experimental vessels when I required this; Miss B. Gilchrist assisted in obtaining and maintaining pure cultures of Chlorella in a healthy state, and also looked after my Cladocera cultures during my absence at Wray Castle.

Dr. Harding has given me as much assistance as I required in the determination of Cladocera, and has kindly read and criticized my systematical notes, though the conclusions these contain remain entirely my responsibility.

I am grateful to Dr. Greenshields and the Metropolitan Water Board for facilities to investigate the Cladocera of the Middlesex reservoirs, and for information regarding the chemical and physical characteristics of such reservoirs from which I have collections.

The staff at the Windermere laboratory of the Freshwater Biological Association gave me every facility I needed during my stay there. I am particularly indebted to Dr. Gilson, who arranged for ~~me to be sent~~ collections to be sent to me from Codale Tarn, and Easedale Tarn; to Dr. Macan who kindly allowed me the use of D.J. Scourfield's manuscript list of the Cladocera records from the Lake District, and also for allowing me to make use of the physical and chemical data contained in his paper on the Mollusca of the Lake District (1951); to Dr. Lund who instructed me in the systematics and identification of algae, and suggested the use of iodine as a precipitating agent; and to Dr. Mortimer and Mr. Mackereth for helpful discussions, and for bringing to my notice their method of measuring temporary hardness.

Dr. Williams of the Botany Department of this college has often assisted me in the determination of algae.

Whilst I was in Denmark, Professor Kaj Berg placed at my disposal every facility of his laboratories. He also kindly read through and discussed with me my views on cladoceran ecology and distribution, and has allowed me the use of some unpublished information. I am also indebted to other members of the Hillerőd staff, who were always willing to assist in any way possible and who have provided me with information on the depths, and pH values of various localities.

I am indebted to the members of the Queckett Microscopical Club for bringing to my attention various methods for the critical illumination of fine objects.

I am indebted to Dr. Pantin for a suggestion which enabled me to overcome the tendency of Cladocera to be caught in the surface film of water.

Mr. Morris of the Geology department of this college reproduced my drawings, and diagrams. ~~and photographs.~~

Part 1. Special Investigations.

One of the principal aims of this research has been to throw some light on what factors determine the spatial distribution of the Cladocera as between localities, and also their temporal distribution within localities. With this aim in view I chose to make a special study of temperature and food. As a consequence of these investigations I was led into a more general study of the factors influencing parthenogenetic reproduction. These different sets of investigations will be treated separately.

Thermal resistance.

Temperature has often been assumed to be an important factor in limiting the distribution of freshwater Cladocera, both locally and on a geographical scale. This idea is supported by the large-scale geographical distribution of many species (a review of the distribution of Cladocera is given by Parenzan 1933, and there are many isolated records of specific distributions in the literature.) Many species are largely or entirely arctic, arctic-antarctic, or arctic-alpine in occurence, such as *Holopedium gibberum*, *Macrothrix hirsuticornis*, *Daphnia hyalina*, being comparatively rare or absent in warmer temperate regions and in the tropics. On the other hand others, such as the species of *Moina*, *Daphnia atkinsoni* and *Macrothrix rosea*, are characteristic of warmer countries. Such distributions at first sight suggest that temperature is a limiting factor for many species. Actually this idea is much too simple, as I hope to show below, and in certain cases even field records indicate that factors other than the direct effects of temperature may give rise to such a distribution. The restricted seasonal occurences of some species, as for instance *Moina* species, which in

England are only known in summer, and the well-known phenomenon of seasonal succession of planktonic species also suggest that temperature may be of importance in the ecology of Cladocera. One might also expect that temperature plays some part in thr restriction of certain species to lacustrine habitats, and of other species to small pools.

There have, however, been comparatively few attempts to investigate this problem. Weis~~s~~mann (1880) and Brown (1929) determined the thermal resistance of a number of species, and attempted to correlate it with the known distribution and seasonal occurence of the species concerned. Weis~~s~~mann's method was to investigate the temperature at which the species died in gradually heated water. Brown transferred his animals suddenly to water at a known temperature and thus determined the temperature in which they died in 1 minute. Both workers claimed that their results showed a general correspondence with the known facts concerning the distribution and occurence of the species concerned. Unbiassed examination of the results shows, however, that this correspondence is by no means exact. Moreover the agreement between the two sets of results is not perfect as Brown himself points out. In Brown's results the low thermal resistance of Daphnia magna and the comparatively low resistance of Scapholeberis mucronata are somewhat unexpected in the light of the known distributions of these species. Both sets of work are imperfect methodologically, since it is not possible to obtain from the results a clear idea of the upper limits of temperature at which the species concerned can survive in nature. Brown's results also suffer from being obtained mainly with animals kept in the laboratory for considerable periods. He claims that this is justified as the Cladocera do not show acclimatization. This statement is probably correct (see below) but he offers no evidence for it. Brown (1929b) also studied the effect of temperature increase on rate of development of several species. He found that in the distinctly warm-water species *Moina macrocopa* and *Pseudosida bidentata* the increase in growth rate between 20° and 30° C. was much more marked than in the other more cold-water species. These two species also differed from the rest in that ~~the growth curves showed no tendency to flatten out~~ the ratio of increase in growth rate over rise in temperature showed no tendency to decrease at higher temperatures. He also investigated inactivation by low temperatures and again found that this occured readily with *Moina macrocopa* and *Pseudosida bidentata*, and less readily or not at all with less pronounced thermophiles. Brown and Crozier (1927) investigated the thermal resistance of a strain of *Daphnia 'pulex'* and of a strain of *Moina macrocopa* more thoroughly, determining the length of time that animals survived throughout the whole range of lethal temperatures. The results are very useful, but unfortunately, owing to the lengthiness of the experiments they could not be repeated on many species or races. McArthur and Baillie (1929) measured the effect of temperature on longevity in *Daphnia magna* and its connection with rate of heart beat, carbon dioxide ~~CO~~$_2$ production, and susceptibility to poisons etc. Their results suggest that each individual expends a constant total amount of energy in its life, and that the shorter life at higher temperatures is a result of the higher rate of energy expenditure. Their culture methods are not above reproach (they used a Banta type medium, see pp 16 & 47), so that the work would bear repeating, but in general it appears to be sound. Pratt (1943) investigated the effect of temperature on population development in *D. magna*, and I shall have occasion to refer to his work below. Comparatively few other authors deal with temperature, but there are a number of scattered observations, of which the most important are those of Banta's School on the occurence of thermal races and mutations in Daphnia palex, referred to below.

A re-investigation of the relation between thermal resistance and occurence of Cladocera seemed to me to be highly desirable, and has in fact yielded interesting results. I concerned myself mainly with the effects of high temperatures, since our facilities for producing constant low temperatures are not very good in this laboratory, but I have been able to make a certain number of observations on the effects of low temperatures.

I decided against the use of short period exposures to high temperatures, as the results obtained by such methods are not easily correlated with the probable effects of high temperatures in the field. They may be of interest physiologically, but they are not very interesting from the ecological viewpoint. On the other hand such experiments as those of Brown & Crozier take far too long to be used for comparative purposes. The period of exposure finally adopted was one of 24 hrs. In most natural habitats high temperatures do not endure consistently for much greater periods than this, so that the period of exposure bears as close a relation as possible to natural conditions. Results obtained by this method could be directly compared with those of Whitney (1939) working on English Ephemeroptera and of Walshe(1948) working on English Chironomidae.

Sources of animals.

As far as possible experiments were performed on animals collected from various field localities on the previous day. My experiments showed that there are considerable differences between strains of the same species, so that results for races from each locality were kept separately. Some information on the general character of these localities is given in P~~p~~art 2 ~~two~~ of this thesis. The source localities were chosen mainly on the grounds of convenience. In a few cases it was not possible to use animals collected in the field and these experiments were performed on animals kept in cultures in the laboratory.

A very considerable literature has accumulated on methods of culturing Cladocera and particularly Daphniidae. Rather extensive discussions or accounts of several methods are given by Vierhoever (1933), by Pacaud (1939) and in Needham, Galtsoff, Lutz and Welch (1937). Various authors have tried to derive an artificial medium of known constitution, which, in addition to a food-supply would only contain distilled water and various chemicals in known amounts. None of these methods is perfectly satisfactory, and in any case the refinement is not necessary for routine cultures. Other authors advocate that Cladocera should only be cultured in their own pond water. This again is inconvenient and not necessary for Daphniidae. For culture water I have consistently used water from Regent's Park Lake, which had been twice filtered and kept in brown glass vessels for not more than ten days.

In respect of food supply the published culture methods fall mainly into three classes. Some, such as those of Banta (1921) (1937), Shipman (1934), Snider (1937), and Heath (1937), depend on the provision of a bacterial infusion, usually of unknown composition, by various methods. In other methods some Alga is provided as food, such as <u>Chlorella</u>, (Fox, Hardcastle, and Dresel 1949) Pratt (1943), nannoplankton (Woltereck), or <u>Chlamydomonas</u> (Pacaud.) A third type of method used by Bond (1934), uses the colourless fungus, yeast. Bacterial culture methods are preferred by most American workers, and Vierhoever (1935) reached the conclusion that these were the best available. However they have never been popular in Europe, most European workers preferring algal methods. Despite Vierhoever's statements, the published literature indicates that bacterial methods are not very satisfactory, at least if egg-number (i.e. average number of eggs per brood) is taken as the criterion of good conditions. Low egg numbers are characteristic of the results of almost all workers who have used bacterial cultures.

I have tried methods of all three types, and have decided that algae are the most satisfactory food. Manure methods, such as those of Banta (1921, 1937) and Hasler (1937) have nothing to recommend them. Unless great care is taken they are apt to prove toxic, and it is impossible to obtain thick cultures with high egg number. A soil-soya meal method was more successful. Several procedures were tried and I shall only give the most satisfactory. 5 gms. of soya-flour were mixed thoroughly with 45 gms. of fine soil, 500 ml of water were added and the mixture stirred. The whole was covered and allowed to stand for five days. The resulting infusion was strained through fine bolting silk and the filtrate kept in a covered beaker. The filtrate remains 'good' for from 10 to 14 days. 1 ml. of this filtrate was added for each 100 ml. of lake-water and the culture animals were placed in the resulting solution. The cultures were changed weekly. It was found that if two or three drops of the undiluted filtrate were added after three days the egg number was considerably increased. Greater strengths of soya filtrate were tried, but these proved unmanageable owing to heavy bacterial growth. The method is reasonably good and much less time-consuming than algal methods, and I have used it for maintaining large stock cultures. However, animals were always transferred to algal cultures some time before an experiment was commenced. This precaution was taken because it was clear that the health of animals in soil-soya cultures was not as good as in algal cultures. It was impossible with the soil-soya cultures to maintain high population densities and the size of individuals remained small and egg-number low (Table 1).

Yeast proved more satisfactory. A suspension of yeast was made up and sufficient of this added to the culture vessel to give the water an opalescent cloudy appearance. More yeast was added, as necessary, to replace that consumed by the Crustacea. Such additions were usually required every two to three days. It has been claimed that fairly constant aeration is necessary when yeast is used as a source of food. In my experience this is not so, if care is taken to avoid excessive concentrations of yeast. If the water is stirred for about 10 seconds and air squirted through it with a pipette once every twenty-four hours, this is quite sufficient to maintain the cultures in good health. As with all other methods I found it advisable to change the culture medium once a week. High population densities can be supported with this culture method, and egg-numbers are quite as high as in algal cultures. The method has however several disadvantages as compared with algal feeding. It is not very easy to gauge the exact amount of yeast required. If a little too much is added the culture rapidly becomes foul owing to the proliferation of bacteria. Under these conditions the culture animals rapidly die, and the development of such a state is so rapid that it is difficult to adopt preventive measures in time. Partly because of this, and partly for technical reasons, it is difficult to adapt the yeast method for standardized feeding. For these reasons I have abandoned this culture method.

The most satisfactory single food proved to be *Chlorella*, a unicellular coccoid green alga, which has been much used, both in this laboratory and elsewhere. It is quite as good a source of food as yeast, and lacks the more striking disadvantages of the latter. Cultures fed with *Chlorella* need stirring once a day to keep the *Chlorella* in suspension, and are best changed once a week; but otherwise they need very little attention. *Chlorella* can be grown easily in pure culture, and the quantity of food given can be standardized if necessary. The pure cultures of *Chlorella* were descended from strains supplied by Professor Pringsheim and by Dr. Fogg. They were maintained on agar slopes containing glucose and salts in the proportions recomended by Pearsall and Loose (1937) and 1.4% agar. Slopemaking and sub-culturing were performed by standard techniques. Originally the initial illumination of new slopes was by means of an ordinary electric lamp enclosed in a bath of water containing a cooling coil. This method is cumbersome, and I replaced it by illumination by means of a fluorescent strip lamp. No protective screening or cooling devices are needed with such lamps as they produce negligible quantities of infra-red and ultra-violet rays. A single $2\frac{1}{2}$ foot strip gave sufficient light, and the colour used was 'warm-white'. When cultures were fed, a suspension was made by washing the *Chlorella* off the slopes with a little water from the culture medium. For stock cultures I did not consider it necessary to add exact quantities of this suspension, and merely added sufficient to maintain a slight surplus. Normally the cultures were fed twice a week.

Provided over-crowding is avoided, animals kept in these conditions are very healthy, and show egg-numbers comparable with those found under good conditions in nature, and considerably higher than are often found in natural populations. Table 1 shows the high egg-numbers and normal sizes attained by several individuals of Daphnia magna from a well-thinned culture.

It is possible that other algae, and particularly some of the nannoplanktonic flagellates might have been even better food; but I found the difficulty of culturing these forms too great for me to use them as a regular food supply. Even maintaining pure cultures of Chlorella involves a considerable expenditure of labour and materials, and so I supplemented my 'Chlorella' feeding by feeding with a mixture of yeast and Chlorella. Cultures fed in this manner were quite as healthy, and almost as easy to maintain as those fed solely on Chlorella. How much more satisfactory this method is than bacterial feeding can be seen by comparing the figures for size and egg-numbers given in table 1 for soya-soil and yeast-algae cultures. In each the animals measured were taken at random from cultures which had been allowed to reach a steady population density. The much higher egg-numbers in the yeast-alga culture are very striking. The mean size of animals from the two populations scarcely differs but it will be seen that there is a significant difference in variability. This is mainly accounted for by the occurence of a small number of very large individuals in the yeast-alga culture, which are not sufficiently numerous to affect the mean. Since the size of Daphnia is partly a function of age, this result suggests that some individuals live longer in the yeast-alga cultures than any do in the soya-soil cultures. I shall deal further with this question of egg-number and longevity in connection with my experiments on reproduction (see below.)

Methods.

My main investigation of thermal resistance has consisted of exposing known numbers of individuals to known, constant, high temperatures for a period of twenty four hours, as stated above. The apparatus used for maintaining such temperatures was a large metal water-bath, heated by an electric heater, and fitted with a cooling coil, a stirring motor, and a toluene-mercury thermostat with a Sunvic control unit. Temperatures above 23° C could be kept constant to within $\frac{1}{4}^{\circ}$ C, with this apparatus, and such temperatures covered the whole range in which I wished to work. The experimental vessels were placed on trays inside the water-bath, some time before an experiment started, in order to reach equilibrium.

Wide-mouthed ~~Hard-glass Pyrex~~ beakers, made of hard Pyrex glass, were used as experimental vessels in order to avoid complication due to oxygen shortage. When 50 animals were used in an experiment, 250 ml. beakers were used, containing 200 ml. of filtered lake-water. When 25 animals were used, the beakers were 150 ml. and contained 100 ml. of water, thus always allowing 4ml. of water to each experimental animal. Whilst this volume of water is by no means optimal (see pages 47,51,53-55, below), it is still considerably greater than is often present in nature or than is commonly allowed by experimenters. Considerations of space prevented my using optimal volumes.

Twenty four hours ~~24 hrs.~~ prior to each experiment the number of animals required, and half as many extra animals, were placed in a beaker containing strained but unfiltered lake-water, 6 ml. being allowed for each animal. This volume was largely determined by the size of available beakers. If more than one animal died during this period, the experiment was cancelled.

Immediately prior to the experiment 50 or 25 animals were counted out into a watch glass and surplus water removed. They were then treated with egg-albumen (see below), and quickly washed into the experimental vessel with a little of the experimental water. The time was then noted. After 24 hrs. the beaker was removed from the water-bath, and quickly cooled to room-temperature by means of a slow stream of cold water. The numbers of living and dead animals were then noted. The surplus animals were retained at room-temperature throughout the period of the experiment, and if any of these died the experiment was cancelled.

The sudden temperature changes involved in this method might be criticized, in view of the statements of several authors, including Lefèvre (1942), that sudden changes of temperature are in themselves rapidly fatal to Cladocera. I have never observed such an effect within the temperature range at which I worked.

At first great difficulty was caused by the tendency of individuals to become caught in the surface film. Individuals so caught ultimately die, so that it was impossible to obtain reliable results. Attempts were made to prevent this by disturbing the surface with an air current produced by an electric fan, but the apparatus was cumbersome and the method inefficient. Dr. Pantin suggested that I should coat the animals with a film of some wettable substance such as egg-albumen, and this was found to be satisfactory. The animals were completely submerged by means of a paint-brush in a freshly-prepared .0001% solution of egg-albumen, and left in it for about 30 seconds, the surplus egg-albumen being removed by means of a fine pipette. The treatment is of course only effective for the duration of one moult. As far as I could determine it had no ill effects whatsoever on the animals. Originally, animals were treated 24 hrs. before the experiment, in order to allow them time to recover from treatment shock. This was found to be impracticable with some races owing to high moulting frequencies. In all later experiments the egg-albumen treatment was given immediately before the experiment commenced. This slight variation in procedure did not appear to affect the experimental results in any way.

Except that obviously unhealthy or moribund animals were avoided, no conscious selection of individuals was made for any experiment, and the animals used can be presumed to have been a fair random sample of the population.

Usually there was no difficulty in determining which individuals were dead and which were alive at the end of an experiment. Occasionally however it is not readily obvious whether an animal is dead or just alive. In such circumstances Brown (1927 a) suggested that animals be counted as dead when the heart has ceased to beat. He justified this by stating that, in his experience, animals never revived once their heart had stopped beating, though they might show unco-ordinated twitchings of gut and antennae for some time. Unfortunately this is not an invariable rule. I have on several occasions noted that animals in which the heart had ceased beating, subsequently revive. In all these cases the animals were still capable of co-ordinated movements when examined. Thus, for my purposes, I have only called animals dead when the heart had ceased to beat, <u>and</u> co-ordinated movement was no longer possible.

I originally intended to perform all experiments on groups of 50 parthenogenetic females but it was not always possible to obtain a sufficient number, so that several experiments were performed on 25 individuals. I had also intended to perform 2 experiments at each of five temperatures, separated by intervals of one degree, on each race. This proved to be impossible for a number of reasons. Populations from which I obtained experimental animals often behaved in an erratic manner, and almost disappeared before a full series of ten experiments could be completed. For a few races the lethal zone was so narrow as to fall well within the range of five degrees, so that it was more informative to increase the number of observations at and near the 50% mortality point, than to perform experiments at temperatures well-removed from this. The opposite difficulty was experienced with some other races where a range of five degrees was not sufficient to cover the whole of the lethal zone. Finally I decided to perform as many experiments as possible, on each race, at whichever temperatures appeared to be the most informative, with the time-saving reservation, that not more than four experiments were to be performed at any one temperature.

I have performed series of experiments of varying degrees of completeness on a considerable number of species, including: Daphnia magna (4 races), Daphnia atkinsoni (2 races), Daphnia pulex (3 races), Daphnia curvirostris (2 races), Daphnia obtusa (3 races), Daphnia hyalina lacustris (2 races), Ceriodaphnia pulchella (1 race), Ceriodaphnia dubia (1 race), Moina macrocopa (1 race), Moina rectirostris (1 race), and Macrothrix hirsuticornis f. arctica (1 race). An effort was made to obtain species differing as widely as possible in their ecological requirements; but limits were set by the nature of the experiments and by the difficulties of obtaining sufficient animals.

If the results obtained from such series of comparative experiments are to be of any value it is necessary that they are not influenced by differences in the behavious of the experimental animals. Otherwise one cannot be certain that an observed difference in lethal death point is real, since the conditions of the experiment are no longer identical. To avoid this difficulty I decided to restrict my investigations to those species/ whose individuals spend most of their time swimming freely, rather than crawling on the bottom, or attached to water plants. This restriction ruled out most species of Cladocera, including such forms as *Sida*, *Simocephalus*, and *Eurycercus*. The inclusion of a species of *Macrothrix*, was perhaps stretching slightly the free-swimming criterion, but observation had convinced me that it spends much of its time swimming an inch or two above the bottom, especially at high temperatures, so that it was fairly uniformly distributed in the experimental vessels. The species of *Bos~~man~~mina* and *Chydorus sphaericus*, otherwise suitable, were not investigated because of the difficulties of applying the experimental technique to such minute forms.

The scope of my investigations was still further limited by the numbers of species available to me in London during Autumn, Winter, Spring, and early Summer in sufficient numbers for experiments. Such species as *Diaphanosoma brachyurum* and *Holopedium gibberum*, though common enought in the north, could not be obtained near London. I was also unable to obtain sufficient numbers of *Daphnia cucullata*, or the very markedly warm-water species *Macrothrix tenuicornis*, either in the field, or by means of cultures.

Nevertheless the species that I have investigated do represent most of the main distributional types of British Cladocera, which might conceivably be connected with temperature.

Results.

The results obtained are given in full in table 2, and the lethal temperatures for 50% mortality, which I shall in future call L.T.50 s. are given in table 3. In most cases the mortality temperature curves are of normal sigmoid form so that these L.T. 50s were readily obtained by means of a probit transformation. This method, described in full by Bliss (1938), and in a condensed form by Fisher and Yates (1948) depends on the transformation of the sigmoid temperature-mortality curve into a linear regression. The L.T. 50 can then be found from this either by calculation or interpolation. Unfortunately it was not possible to deal with all my results in this simple manner. With several races, including *Daphnia carvirostris* (Zoo), *D. magna* (Zoo), *Ceriodaphnia dubia* (Regent's Park,) and *Moina macrocopa* (Aldwarke), it was clear that, even when full allowance was made for variability, the results could not justifiably be fitted to a sigmoid curve. In all these cases the best fitting curve was one that could be best described as a bimodal sigmoid curve, as shown in figure 1. In the case of *Daphnia curvirostris* and *Daphnia magna* from the Zoo, a possible explanation was that increasingly severe conditions in the source habitat had brought about a differential selection of individuals with respect to thermal resistance, since the experiments at higher temperatures were carried out at later dates. In all the later experiments this possibility was avoided by randomising the dates at which the experiments were conducted. Nevertheless the same effects were shown by some races. In fact the effect is even more striking in the case of Moina macrocopa. It seems to be a real phenomenon and not due to any defects in the experimental method. I have been told that some strains of Daphnia obtusa show similar bimodal response to toxic substances, but I can find no records of similar phenomena in the literature. The obvious explanation is that the strains in question are examples of physiological polymorphism. Whilst this cannot be ruled out, it is probably not the true explanation, since the results remain remarkably constant over considerable periods of time despite changing environmental conditions. It is not easy however, to think of a really credible alternative explanation. Possibly it is due to differential effects of increasing temperatures on several factors some of which tend to cause death whilst the others, which become of importance at intermediate temperatures favour survival. Whatever the true explanation of this deviation of the curve from the ordinary sigmoid form, it makes it impossible to assess the 50% lethal point by means of the probit transformation. In these cases then I have determined the L.T.50s. by direct interpolation. These figures, indicated in the table by asterisks, are thus somewhat less exact than those obtained for the other species, but are sufficiently accurate for comparative purposes.

Before proceeding to discuss the results comparatively, certain general aspects can be pointed out. With the exception of the Berrylands race of Daphnia atkinsoni all the races have a comparatively high degree of resistance to high temperatures. This is clear when my results are compared with those which Whitney (1939) obtained for ephemeropterans. Almost all my races have thermal resistances, comparable with those of the most heat-resistant species of ephemeroptera. This is in good agreement with their limitation to ponds and lakes, since both Whitney and Walshe(1948) concluded that stream species in general were less resistant to high temperatures than pond species. Some other invertebrates are even more sensitive to high temperatures than those investigated by Whitney, for instance the spring inhabiting forms such as the larval trichopteran *Apatidea muliebris* (A. Nielsen, personal communication) and *Planaria alpina*, and the marine invertebrates investigated by Fox etal (1936 to 1939). On the other hand the littoral gastropoda show high resistance to heat (Evans 1948), apparently comparable with that of Cladocera species. The general pattern of my results is thus in agreement with the general conclusion that groups of animals inhabiting more extreme conditions are usually more resistant to high temperatures. It is noteworthy also, that as with the littoral Gastropoda, most of the forms that I have investigated can withstand temperatures far higher than any they are ever likely to meet with in normal conditions. The highest temperature that I have ever actually recorded in the field was 28°C, though it is probable that some very small waters may reach 30°C for short periods in the middle of the day. It is certain that even temperatures as high as 30°C are rarely maintained throughout a period of 24 hours, and 27 to 28°C can be taken as the normal average temperature for small ponds in very warm weather. It is clear that that the Berrylands race of *Daphnia atkinsoni* which inhabits a small temporary pond, could not survive in such a pond in hot summer weather, and it is just possible that temperatures might rise high enough in some ponds to be lethal to *Macrothrix hirsutricornis f. arctica*; but on the whole it is clear that the direct lethal effects of high temperatures can not be of any great importance in determining the distribution of Cladocera.

Though these direct lethal effects are not of great importance, it might still be that the L.T. 50s are correlated with the geographical and ecological distribution of the species and varieties. Examination of table 3 shows that such correlation is not very well-marked in the species that I have investigated. Of these species, the two species of *Moina* are distinctly thermophilic in distribution, are absent from the north of the British Isles, generally rare in Northern Europe, and only occur in summer in small shallow pools and other warm bodies of water. In England *Moina rectirostris* has been found in temporary ponds, and it is common in such habitats in more southerly countries; but it is very rarely found in non-permanent ponds in Denmark, and Berg (1929) suggests that this might be due to its need for high temperatures. *Daphnia atkinsoni* is another definitely southern species. It is quite common in the Mediterranean region and S.W. Asia, but is very rare and sporadic in the British Isles and N. Central Europe, and extremely rare in more northerly regions, though it has been found in Sweden, Iceland, and Denmark. Like the *Moina* species it is only found in small shallow pools of the type that become very warm in summer, and less commonly in small temporary pools. *Daphnia magna* and *Ceriodaphnia dubia* are less distinctly southern, warm-water species. The former is found according to Scourfield and Harding (1941) in small ponds and small shallow bays of larger waters, though in my experience it may sometimes occur generally distributed in larger bodies of waters (see below). It may be found throughout the year but is distinctly less common in winter than in summer, it is found throughout temperate Europe but becomes rarer in the North. It must be noted that Brown (1929a) claims that it is a cold-water species, but this statement is in direct conflict with the opinions of all other workers. *Ceriodaphnia dubia* is an extremely widely distributed species found from Patagonia (Ekman, as *C. limicola*)to Sweden (Lilljeborg 1900, as *C.affinis*) but, judging from published records, it is rather more common in the tropics and in warm temperate regions, than it is in cool-temperate regions. In England it is a southern and eastern species. It is a summer species, though less markedly so than the species of *Moina*, and, though it may occur in late spring and in autumn, it is never found in winter. On the other hand it is definitely a lacustrine form, never occuring in very small ponds, and being characteristic of small lakes and large ponds. Regent's Park Lake, the source of my race, is a somewhat typical habitat in size. Such waterbodies whilst reaching higher temperatures than large lakes, never reach the very high temperatures sometimes shown by small ponds. Of the other species *Macrothrix hirsuticornis f. arctica* is distinctly a cold-water form. The species as a whole is very widely distributed, being found from the arctic to the antarctic. In the arctic and sub-antarctic it is widespread, common, and often very abundant; it is rare and local in cool-temperate regions; very rare and local, and largely confined to upland areas in warmer countries. In the arctic all strains are of the form *f. arctica*, but this form is extremely rare elsewhere. Apart from my Hampshire locality it is known from the Italian mountains (Parenzan, 1932) and from Denmark (Berg 1933). It is difficult to define the habitat range of the species as a whole, but my locality for the form *arctica*, as that of Professor Berg, is a small, shallow, pool which persists into early summer but dries up in the warmest weather. *Ceriodaphnia pulchella* is widely distributed in temperate regions, becoming rare towards the arctic, and towards the tropics. It is principally a lake species but may occur in small pools, and my specimens were from such a habitat. Daphnia hyalina is also a northern species but less markedly so. It is not found in the arctic or in sub-arctic regions, but it is common in north Europe, and the Alps. It is rare in the lowland areas of west and central Europe. It must be noted that its distribution can be explained on grounds other than reactions to temperature. It occurs throughout the year but more commonly in summer. It is very definitely a lake species, and is rare in small ponds. Regent's Park Lake is a rather small habitat, whilst the Children's Boating Lake is a very small habitat for this species. The other three species of Daphnia are all widely distributed forms of temperate regions. Only Daphnia pulex occurs in the arctic, and all three are rare or absent in the tropics. All occur throughtout the year, though tending to be less common in winter than in summer. Of the races that I have investigated only the Berrylands race of D. obtusa remains abundant throughout the winter. D. obtusa and D. curvirostris are found normally in very small shallow pools, and all my strains were from such habitats. D. pulex is a species of somewhat larger pools, though, rarely, as in Bedford College Botany Garden, it may occur for a time in pools of the sort normally associated with the other two species.

One of the races investigated deserves special mention, the race of D. magna from the Wellcome Institute. This strain was descended from individuals obtained from the zoological gardens and had been kept for several months at a temperature which never deviated far from 27-30°C. I included this strain in my series to test whether or no there was any appreciable acclimatization or adaptation to high temperatures. This race has an L.T.50 quite comparable with other races of the species. There is no evidence of any acclimatization or adaptation to high temperatures. Brown (1929 a) had previously stated that Cladocera do not show acclimatization, but he gave no evidence in support of his contention.

From the data given of the distribution of the species, and occurence of the races investigated, it is possible to predict the sort of thermal resistance each should have, if thermal resistance were correlated with distribution. I have included such expected lethal points, expressed in the convenient general terms, high, medium, and low, in table 3. Since such estimates are subjective, it is impossible to avoid bias in making such assessments. In practise I have assigned all doubtful cases to the class which accords best with the experimental results. Nevertheless, it is very clear that there is very little correlation between observation and expectation. The highest L.T. 50 belongs to the southern, warm-water species *Moina rectirostris*, and *Moina macrocopa* also shows a high value; but the lowest L.T. 50 of all belongs to the Berrylands race of the southern, small-pool, species *Daphnia atkinsoni*. The lacustrine *Daphnia hyalina* shows lower L.T.50 s than most of the other species, but they are not markedly lower and fall within the range covered by the races of *Daphnia pulex* which are races from small waters. If the results are considered by habitats the correlation is not greatly improved. The somewhat striking difference in L.T. 50s of *Daphnia hyalina* and *Ceriodaphnia dubia* from Regent's Park Lake, may be noted, in this connection (see tables 2+3)

My general conclusion is that, except in the case of the two species of *Moina* and perhaps, also *Macrothrix hirsaticornis f. arctica*, the forms that I have investigated show no correlation between their distribution and their resistance to high temperatures. This conclusion is directly opposed to those of Weis~~s~~mann and of Brown, but as I have indicated above the discrepancy is rather between our conclusions than between our results. I at least do not find the results of Weis~~s~~mann and of Brown provide convincing evidence for postulating a correlation between thermal resistance and distribution. This lack of correlation is a further point of agreement between my results and those obtained by Evans (1948) for littoral Mollusca.

It is noteworthy that in several species the different races have L.T.50s differing as much as do those of species. The most striking instance is provided by the two races of <u>Daphnia atkinsoni</u>; but similar, though less marked differences occur between the strains of <u>D. pulex</u> and <u>D. hyalina</u>. The Berrylands race of <u>D. atkinsoni</u> is quite anomalous in its reaction to high temperature, and it shows several other peculiarities. Parthenogenetic reproduction is very poor in cultures kept in the laboratory at temperatures above 20°C, whatever the conditions of food supply or crowding; but vigorous bisexual reproduction occurs. At these temperatures it is quite impossible to maintain pure parthenogenetic cultures in the laboratory, but these can be maintained at lower temperatures. In natural conditions the race flourishes during the winter, if the food supply is satisfactory, but when the water becomes warm in early summer parthenogenetic reproduction gives place to bisexual reproduction, and unless the season is very cool, the race ultimately dies out before the pond finally dries up. The race is thus well-adapted to its habitat, a small temporary pool drying up in early summer. There is some evidence that the strain of <u>D.atkinsoni</u> found at Berrylands, is representative of a low-temperature race, widespread in western Europe. Professor Berg told me that in most localities in Denmark, *D. atkinsoni* dies out, as soon as the water-temperature of the pools which it inhabits rises much above 20°C; he also told me that in France, ~~Professor~~ Dr. Pacaud has never found the species when the water temperature has been high. Though these observations cannot be conclusive they strongly suggest that this low-temperature race is commoner in Western Europe than the form with 'normal' thermal resistance. That it is not the only form which occurs is shown by my Hampshire race; and whilst I was in Denmark ~~this~~ last summer, Professor Berg showed me specimens of *Daphnia atkinsoni* from a pool in Jutland, where the species appears to occur throughout the summer. I have not been able to detect any morphological differences between these two thermal races, and if there are any they must be very slight. The high variability of the species may well obscure differences which do exist. Special thermal races do not appear to be uncommon in the Cladocera; the Banta school having recorded several (Brown 1929a, Banta and Wood 1928, Banta 1949). One of these, a low temperature race of *D. pulex*, shows a very similar behaviour in respect to temperature to my Berrylands race of *D. atkinsoni*. The occurence of such a low temperature race in *D. atkinsoni* is of great interest in view of the distribution of the species. It has often been suggested that the occurence of this species in northern countries was accidental, and that it failed to establish itself generally because of the lack of sufficient habitats which reached high enough temperatures for it to thrive. The occurence of this special low-temperature race is good evidence that the species is permanently established in northern latitudes, in agreement with the views of Berg (1931).

Clearly, too, whatever is responsible for its rarity in these areas, it is not temperature. Indeed the low-temperature race is less adapted to high temperatures than the northern species *D. hyalina*, and cannot live at high temperatures which occur rather commonly in small ponds in Britain and Denmark. In anticipation of results to be mentioned below, I can point out that low winter temperatures are not in themselves greatly unfavourable to the species, or at least to the low-temperature race. This race occurs throughout the winter at Berrylands. In the laboratory individuals live indefinitely at temperatures between 0°C and 2°C though growth is slow, and reproduction does not seem to occur at temperatures much below 6°C. It remains a puzzle, for which no satisfactory reason can be given, that this species should nevertheless be almost completely confined to those habitats which reach the highest temperatures in summer.

Banta and his school have noted several thermal races of *Daphnia*, which have appeared in their cultures, or have been investigated from the view-point of sexual reproduction. One mutation of *D. longispina* gave rise to a strain adapted to high temperatures. Another race, of *D. pulex*, was a low temperature race showing many points of similarity to my race of *D. atkinsoni* (Banta 1949, Brown 1927 etc.). Thus it had a comparatively low thermal death-point, showed predominantly ephippial reproduction at ordinary room temperatures, and parthenogenetic reproduction at lower temperatures. The well-known thelytokous races of arctic Cladocera are presumably also primarily adapted to the peculiar temperature conditions of the arctic, which necessitate a somewhat unusual pattern of reproductive activity. My results for *Moina macrocopa*, when compared with the observations of Brown and Crozier (1927) for the same species, indicate that there are thermal races in this species also. Brown and Crozier's race lived and reproduced normally at 39°C, a temperature higher than was necessary for 100%mortality in 24 hrs. with my race. Thus races which show direct or indirect temperature adaptations are by no means uncommon in this group. This comparative frequency of thermal races emphasises the contention that direct effects of temperature are not of paramount importance in determining the distribution of Daphniidae. It is of interest that it is associated with feeble or none existent powers of acclimatization.

It was possible that resistance to low temperatures would prove to be correlated with distribution, even though resistance to high temperatures showed such poor correlation. As mentioned above Brown (1929 a) investigated this problem, and showed that, whilst certain warm-water species such as Moina macrocopa are rapidly inactivated by temperatures well above freezing-point, cold-water species such as Daphnia pulex could remain active indefinitely at 0°C. It is a well-known fact that many species of Cladocera including Daphnia pulex, Daphnia obtusa, Daphnia longispina, Daphnia hyalina, Simocephalus vetulus, Sidacrystallina, Bosmina longirostris, Macrothrix laticornis, Alonaquadrangularis, Alona affinis, Chyderas sphaericus and many others can survive for considerable period s in ice-covered waters. I have found most of these myself in such circumstances. On the other hand some species such as Moina spp and Ceriodaphnia dupia are rarely or never found in winter, and it would be of interest to know how well these can stand low temperatures.

Unfortunately it is very difficult to investigate the effects of low temperatures in a laboratory which has no constant temperature rooms. A refrigerator can be used as a substitute for these but it is not very easy to maintain it at an even approximately constant temperature. However, I have been able to obtain some results by using the refrigerator in cool weather only. It is unfortunate that the method could not be used in hot weather, owing to the large fluctuations of the internal temperature of the refrigerator, since this greatly limited the number of species which could be investigated.

As was to be expected, in view of field records, it was found that a considerable number of species, including all the species mentioned above as well as *Macrothrix hirsuticornis*, *Daphnia magna*, and *Daphnia atkinsoni* survived indefinitely at temperatures between 0°C and 2°C. On the other hand several species were rapidly killed at this temperature, including *Moina macrocopa*, *Moina rectirostris*, and *Ceriodaphnia dubia*, *Ceriodaphnia dubia*, however, survived and reproduced at 8°C, but the two *Moina* species were killed by this temperature.

I shall deal with the effects of temperature on reproduction at length in my account of my experiments on this problem, but reproduction at these very, low temperatures is most conveniently treated here. Those species that survive indefinitely at temperatures near freezing-point can be divided into two groups, those in which reproduction proceeds at the lowest temperatures, and those which merely survive without reproducing. The former group is extensive, and in my experience includes *Daphnia hyalina*, *Daphnia pulex*, *Daphnia obtusa*, *Simocephalus vetulus*, and *Chydorus spaericas*. All save *Daphnia hyalina*, are somewhat commonly found under ice, and this species has been recorded on a considerable number of occasions as living under ice. Some species which I have investigated did not reproduce at low temperatures. I have failed to obtain reproduction in cultures of D. magna kept for any length of time at temperatures below 6°C. This agrees with the opinion of Berg (1931) based mainly on field collections, that this species does not reproduce at temperatures of less than 6°C. My field observations are also in general agreement, though not absolutely so. On 6.2.51, and again on 28.2.51, I obtained young and adult individuals, some with numerous eggs, from King George Vi reservoir, Middlesex (a most unusual habitat for this species.) On both occasions the water temperature was about 4°C, and the Water Board biologists inform me that this temperature had remained rather constant for several weeks. This seems to be another instance of the well-known phenomenon of a species withstanding adverse conditions more successfully in the field than in the laboratory. Another species which will not reproduce in the laboratory at very low temperatures is Daphnia atkinsoni, but this species certainly reproduces at just over 0° C in the field.

The general impression given by these results is that there is a very good correlation between the seasonal occurence of species of Cladocera and their resistance to very low temperatures. The most resistant forms are those which commonly occur in winter; the least, those which only occur in summer. Unfavourable seasons are thus passed solely as resting eggs. On the other hand there appears to be comparatively little correlation between resistance to low temperatures and geographical and ecological distribution, at least in so far as those species occuring in the British Isles are concerned. A considerable number of species, notably Daphnia obtusa, *D. hyalina*, and *Macrothrix laticornis*, which can withstand low temperatures very easily, are, nevertheless absent from the arctic. Similarly *Daphnia magna* seems less well adapted to low temperatures than *D. atkinsoni*, though it is commoner in northern latitudes. The lack of correlation between resistance to low temperatures and type of habitat is even more striking. In particular there is no evidence that lacustrine species, such as *Daphnia hyalina*, are less resistant than pond species such as *Daphnia pulex*. The greater degree of correlation between temperature resistance and seasonal occurence, than that which occurs between temperature resistance and spatial distribution, is perhaps connected to some extent with the ready production of resistant resting stages, found in most species of the group which enables them to survive unfavourable conditions.

Throughout the above discussion it will have been noted that the species of *Moina* stand apart from the other species investigated in showing very marked correlation between their distribution (southern), their seasonal occurence (summer), their habitat (small ponds), and their temperature resistance (easily killed by low temperatures; very resistant to high temperatures). Judging by Brown's results a similarly high degree of correlation can be expected for *Macrothrix tenuicornis*, also a pronouncedly warm-water species. Thienemann (1926) suggests that one of the factors limiting the distribution of *Holopedium gibberum* is inability to stand high or low temperatures, and the distribution of *Ophryoxus gracilis* strongly suggests that it is similarly limited. Unfortunately I have been unable to obtain these species in sufficient numbers to test these conclusions experimentally. These forms are, however, exceptional, and do not undermine the general contention that the direct effects of temperature on survival are of comparatively little importance in influencing the distribution of the Cladocera in Europe.

Reproduction in relation to temperature and other factors.

Whilst direct lethal effects of high temperatures did not seem to be of great importance in the ecology of the Cladocera, it seemed to me to be likely that the effects of temperature on reproduction would be of some importance. This idea was strengthened by the fact that the seasonal replacement of one species by another sometimes seemed to be correlated with temperature. Instances of such replacements can be found in almost all extensive series of data on planktonic cladocera, particularly those of small waters (see for instance Wesenberg-Lund 1904 - 1908, 1926, Berg 1931), and I have come across several striking examples among my own collections. In Regent's Park Lake, the burrowing species *Leydigia leydigi* is found throughout the colder part of the year, but is replaced by *Leydigia acanthocercoides* in the summer. Similarly in 'The Wash', Aldwarke, S. Yorkshire, *Daphnia curvirostris* is abundant in late spring, early summer, and early autumn, but during hot periods in midsummer it may be completely replaced by *Moina macrocopa*. In both these instances the cool-water species can survive at higher, and the warm-water species at lower temperatures, than those at which they are normally found in these localities. It seems probable that differential effects of temperature on reproduction were the cause of the replacement of one species by the other. I decided to investigate the influence of temperature on reproduction; but it soon became clear that if the results obtained were to have any value, other factors must also be investigated.

As I pointed out in the introduction, the unusual reproductive behaviour of the Cladocera has long been the subject of intensive investigation, but this investigation has been almost entirely concerned with the factors controlling the occurence of sexual reproduction. Temperature has been studied as one of these possible factors, and a considerable body of data has been accumulated in this connection (see for instance Berg 1931, Banta 1939, Brown and Banta 1932, Grosvenor and Smith 1913). It seems to be generally agreed that, within wide limits temperature is of little importance, but that outside these limits it may be a decisive factor in initiating sexual reproduction. In most cases the zone of high temperatures favouring sexual reproduction seems to be a narrow one including temperatures just below those of the lethal zone. However for a few races this zone seems to be quite extensive and to include temperatures as low as 20°C (see above.) The results of Banta and his co-workers indicate that low temperatures may also bring about sexual reproduction if they act through a sufficient period, though they are apparently not so effective as other factors. The fact that in natural populations sexually reproducing individuals are most commonly found in autumn when the temperature is falling is well-known, but it appears in many cases to be attributable to factors other than temperature (Wesenberg-Lund 1905-10, Berg 1931, Poulsen 1940 b. etc.) Thelyotokous races of Cladocera have also received some attention (Banta 1925, 1939, Poulsen 1940 a, 1940 b, Olatsson 1918). In these races resting eggs are produced regularly, but are usually or invariably produced parthenogenetically. Males are either unknown or very rarely observed. The interest of these races in a study of temperature effects is distributional. The vast majority of arctic Cladocera appear to be thelyotokous but, to my knowledge, only one such race is certainly established as occuring in warmer regions (the Cold Spring Harbour race of Banta 1925). I can find no useful information on other aspects of the physiology of these races, but the distribution leaves little doubt that thelyotoky is an adaptation to the peculiar temperature conditions of arctic waters.

It is clear from the literature that the effects of temperature on sexual reproduction could be of importance in the ecology of the group; though it is not clear as to how far they are important in natural conditions.

Parthenogenetic reproduction has been much less studied in this group, though it presents features which might well have attracted attention in any other group, and was first studied by Jurine in 1820. It is well-known that in all Cladocera, except the members of the Chydorinae the number of young produced in a brood, which I shall call the egg-number, is very variable, though except in the Eurycercinae, the number of resting or ephippial eggs is small and definite. In the Chydorinae only 2 parthenogenetic eggs are produced at any one time. More rarely the egg-number may be one, but usually individuals have 2 eggs or are 'empty'. I have not noticed any references to higher egg-numbers in the literature, but I have seen occasional individuals of Leydigia leydigi with three eggs. This however is clearly a highly unusual phenomenon. It is obvious from field collecting, and from observation of cultures, that variation in egg-number is due largely to environmental conditions, though there are admittedly limits to the number of eggs that may be produced by individuals of any given race. In passing, I may note that these limits do not seem to be adequately known for any race, with the possible exception of Pratt's (1943) strain of Daphnia magna. This theory of the environmental control of egg-number is now generally admitted to be unassailable, though a few authors as Stephanides (1949) seem to be unaware of its implications, and still erroneously use egg-number as a racial distinction. Little however seems to be known of the exact roles of different environmental factors in determining egg-number. It is rather commonly assumed that one of the most important of these, if not the only one of any importance, is the abundance or scarcity of suitable food. Numerous papers have shown that the level of feeding can have a profound effect on egg-number, as those for instance of Brown and Banta (1935), of Lefèvre (1942), of Berg (1931), of Fox (1948), of Schultz (1928), and Fox, Hardcastle and Dresel (1949). The evidence is not sufficient nevertheless, to justify the assumption made, for instance by, Fox, Hardcastle and Dresel (1949), that egg-number can be taken as a reliable index of good or bad nutrition. Such usage ignores the effects of other factors, which may be, and I hope to show are, of considerable importance. Most authors only refer to egg-numbers incidentally, and there are very few accurate studies of parthenogenetic reproduction in relation to any factors.

Pratt (1943) has made a very close study of population development, and parthenogenetic reproduction in D. magna at three temperatures (12°C, 18°C, and 25°C), and his results are of great interest. He was able to show that at 25°C his populations showed periodical fluctuations in numbers which were not due to external factors, but were dependent on the nature of reproduction in this species. At 18°C the populations developed in a more normal fashion building up to a constant level. At 12°C he was not able to followin the population development right through owing to the very slow rates of reproduction. Experiments on the egg production of isolated individuals convinced him that these phenomena were best explained on the basis of crowding effects, presumably operating through conditioning of the medium during the two day periods in which it remained unchanged. He showed that crowding in early life could affect the egg production throughout life. Unfortunately he was not able to standardize the amount of food he gave completely, but he considered that effects of food had been minimized, since he always added sufficient food to maintain a surplus, My observations indicate that this was not necessarily so, since underfed animals still may not consume all the food available, but this possible source of error does not seem to have affected his results.

Schultz (1928) made a study of the effects of light on various activities of Daphnia. Many of his results are clearly not valid, as for instance his conclusion that light increases the development of red pigment, which he attributes to caretenoids, and his data are very poorly presented. For these reasons his conclusions seem to have been generally ignored. He states that individuals reared in darkness show lower eggnumbers than those reared in light, a statement that I have been able to confirm, and Lealso states that they attain a larger size. Variations of egg-number with age have been recorded by Ingle, Wood and Bantal (1937), Banat (1939), Anderson, Lumer, and Zupancir (1937), and Anderson and Jenkins (1942).

The fertility of Cladocera does not, of course, depend solely on the egg-number. It is also affected by the time taken to reach maturity, the frequency of moulting of the adults, and the length of life. All these are affected by environmental conditions, though as Banta (1939), and MacArthur and Baillie (1929) have shown, they are not independently variable. The physiological age of an individual is determined by the number of instars it has passed through, so that the age at which maturity is reached and the mean length of life are more or less constant unless the length of the instar varies. Banta (1939) found for his strain of D. longispina that the individuals became mature at the 5th instar in all cases, but Anderson (1932), and Anderson, Lumer and Zuppancir (1937) showed that the instar at which maturity is reached may vary within narrow limits, Banta's (1939) study is one of the few comprehensive studies of fertility on any Cladocerans. It involved strains of Daphnia longispina, individuals of which were kept under 'ideal' conditions (1 individual to 100 ml. of food medium) at 25° C. The mean total number of young produced per individual varied from 270.2 to 319.9, individuals were mature at the 4th instar and there were from 10 to 19 instars in a life span. Banta also determined the numbers of young produced per instar, the growth rate during instars, and the length of instars. He noted a sudden increase in instar length at the first adult instar and thereafter a slow progressive increase throughout life. He attempts to correlate the instar length with the number of eggs produced per instar and the growth-increment, but his conclusions are not very convincing. His figures give the instar length of adults as from 36 to 63 hoars. A similar study is that of Anderson and Jenkins (1942). Working on D. magna, they found that at 25°C individuals became mature at the 5th to 7th instars. They note as Banta did, slight progressive increase in instar length during adult life though admitting there is much variation; the length of and instar varying from 47.8 ± 0.2 to 76.4 ± 1.1. It is of some importance in this connection that they used a medium similar to that of Banta. They found longevities from 944 ± 32 to 990 ± 43 hours.

MacArthur and Baillie (1929 a & b) studied the effects of temperature on various metabolic processes of Daphnia magna and their connection with longevity. They concluded that individuals die after having consumed a fixed amount of energy as measured by number of heart-beats etc. They noted that the actual length of life of individuals was very variable even at the same temperature. For females the mean length of life was 29.24 ± .44 days at 28°C, 44.73 ± .45 days at 18°C, and 108.41 ± 3.93 days at 8°C. For males the figures were slightly less, especially at higher temperatures. Instar lengths varied correspondingly, the mean for females at 28°C being 72 hours.

Dresel (in Fox, Hardcastle and Dresel 1949) determined the length of instars in Daphnia obtusa at 25°C. She found that the mean length was 52 hours. Unfortunately no information is given as to the number of individuals involved in making this estimate, or the conditions under which they were kept. The length of instar given is distinctly short when compared with other published results, as also with those which I have obtained.

It is difficult to make an assessment of these results, based as they are on different species, investigated at different temperatures, under different general conditions of culture and crowding; and a consideration of them is best postponed until after I have dealt with my own results, which are not always in agreement with those of the authors mentioned.

My experiments on reproduction fall into three series, which can be conveniently referred to as three experiments. The principal aim was to investigate the relation between temperature and fertility and reproductive rate. Preliminary experiments suggested that other factors, as food-supply and degree of crowding ought also to be considered, whilst experience gained in the first experiment suggested that light might also have important effects on fertility.

Experiment A.

This experiment was designed to investigate the effects of temperature and crowding on the reproductive rate of Daphnia magna. Two temperatures were chosen 27°C and room-temperature (c. 18°C Room A.) I had hoped to obtain a third temperature by making use of a basement room (Room B), but the temperature of this room proved to be on the average as high as 17°C. It was more constant than the temperature of room A. Conditions differed slightly in the two rooms in that room B was almost always dark, whilst room A had normal lighting. A temperature of 27°C was maintained, as described above, by means of a constant temperature bath. During this first experiment no special precautions were taken to control the amount of light reaching the animals kept in this bath, which was under the same conditions of lighting as the rest of the room~~, A. (below)~~.

Insert A (p. 50).

The experimental animals were kept in pyrex glass beakers, containing 200 ml. of filtered lake water, the water being completely changed, and any young produced removed, every two days. One beaker at each temperature contained 12 individuals. For the purpose of this experiment I am calling this crowded conditions, though the degree of crowding is almost negligible compared with conditions which are commonly found in nature, or which have often been used in experiments. For experimental purposes this relatively slight degree of crowding has several advantages. It is not sufficient for the animals to have much effect on the oxygen tension of the water, and so removes doubts of possible complications due to low oxygen concentrations. An adequate food-supply can be maintained without the necessity for very high concentrations of the food-organism, in this case <u>Chlorella</u>, which might cause accumulations of deleterious products (see Lucas 1947). The low egg-numbers recorded by workers who have used highly crowded cultures (e.g. Fox 1948, Fox, Hardcastle Dresel 1949, Pratt 1943) show that a high degree of crowding has very marked effects on egg-number, but it is of interest to learn whether these effects appear at lower concentrations.

4 other beakers contained three animals each. These I shall call uncrowded cultures. A volume of about 67 ml. per animal is presumably optimal for this species or very nearly so. Banta (1939) and Macarthur and Baillie (1929) regard the optimal density as being about 1 individual to 100 ml. and the latter authors declare that even so low a density as 1 animal to 40 ml. is distinctly less favourable. These statements are unfortunately not very reliable for two reasons. The Banta culture method is not fully satisfactory, and the egg-numbers given by Macarthur and Baillie suggest that in their experiments the animals were certainly inadequately fed. Also these authors were not only varying the concentration of their cultures, but also the amount of food available per animal. Nevertheless their results did indicate the most likely region for optimal concentration, but it seemed unnecessary to use so high a

volume as 100 ml. per animal, especially since this would have been inconvenient from a practical view-point.

These four uncrowded cultures at each temperature together corresponded to one crowded culture, and the records from them were pooled, since no obvious increase in precision would have been gained by treating them separately.

As food-supply I used a pure culture of Chlorell a vulgaris. Standard suspensions of this algae in culture water were made by a modification of the technique described by Fox, Hardcastle, and Dresel (1949). In this method the suspension of Chlorella is matched against a standard consisting of 4.5 ml. of a saturated solution of nickel sulphate, .5 ml. of a saturated solution of potassium chromate, and .2 gms of Keiselquhr, made up to 20 ml. with distilled water. The method has several disadvantages, and I later abandoned it in favour of a more direct method of measurement, but with care it can be used consistently. The standard must be freshly made up as required, since in rapidly deteriorates on standing. It must be thoroughly shaken before each comparison since the Keiselquhr sediments rather rapidly, and it is then impossible to obtain an exact match. The tube used for the standard must be thoroughly cleaned immediately after use. Otherwise the glass aquires a faint yellow stain, which upsets estimations, and is extremely difficult to remove. The Chlorella suspension was added to the culture vessels every two days, immediately after changing the water. The volume added per individual was always .1 ml. Thus I could be sure that any effects I observed were not due to relative shortage of food. An unavoidable complication is the necessity for having higher concentrations of

Chlorella in the crowded cultures. This will tend to make it easier for the individuals to obtain an adequate food-supply. It will thus tend to mitigate the effects of crowding.

During the course of the experiment a number of animals died. The deaths were noted and the experiments continued, but the volume of culture medium, and the amount of food given were adjusted accordingly.

Owing to shortage of time it was not possible to continue the experiments throughout the life of the individuals, and so they were discontinued at an arbitrary time of 24 days. The experiment was designed to give information on the following points: total egg-production, or rather total production of viable young, in a given time; frequency of moulting, and hence length of instar in the adult; and the average number of viable young produced per individual, i.e. the average egg-number. Originally I intended to determine the egg-numbers of each individual directly. Preliminary trials showed that it was not possible to do this accurately where the egg-number was high, without dissecting out the eggs, which would probably have damaged the parent. Even with low egg-numbers the disturbance involved in making the count was not desirable. I was thus forced to adopt the indirect method of counting the number of young produced in a two day period, and the number of exuviae. The ratio of these gives the average egg-number. Since the exuviae sometimes become separated into several portions the number of carapace valves was counted, since these were the most readily recognizable fragments. Some difficulty is created by the fact that the young are released a short, and somewhat variable, time before the moult (see Dresel 1948, Fox, Hardcastle and Dresel, 1949). I overcame this by noting the number of 'empty' females with large ovaries, such females being easily identified by the naked eye, and adding these to the number of exuviae recorded. At the end of the next two day period, and equal number was subtracted from the number of exuviae found.

Insert at A.

In view of Pratt's (1943) results I thought it desirable to commence all my experiments with neonatae or second instar individuals (it is not easy to distinquish these with certainty, and is of little importance since the first instar is of very short duration, and also the young are not always born at precisely the same stage of development.)

It was also possible from the observations to determine roughly the time at which the first brood of young was produced.

The results obtained are given in tables 4 to 7. Table 4 gives the actual data in a condensed form; the other tables are derived from it and designed to show various features of the results more clearly. The frequency of moulting, the rate of ~~/~~egg-production and the variations in average egg-number are shown graphically in figures 2 to 5. The figures given for average egg-numbers were obtained directly from the observations; but it was necessary to correct the figures for total egg-production, and for total number of instars in a given time in order to remove the spurious falling off in rate of increase caused by the diminished numbers of surviving individuals in the later part of the experiment. All increments observed in these quantities were reduced to those which would have been given by twelve individuals in which they showed the same rate of increase. The later figures are thus to a certain extent less reliable than the earlier ones; but this is not of great importance, since they show no

~~peculiar~~ features apparently attributable to methodological errors.

Table 5 and figure 2 show that the effect of temperature on total egg production is very complex. At 18°C the total number of young produced in twentyfour days is actually greater than the total number of young produced in the same period by animals under comparable conditions at 27°C. On the other hand egg-production commenses earlier at 27°C. The rate of egg-production is thus greater at 18°C than at 27°C. In this race, under these conditions, the two rates of egg-production do not differ very greatly so that it is only for life-spans of more than twenty-one days that the egg-production at the lower temperature exceeds that at the higher temperature. A striking feature is the distinctly lower reproductive rate of the animals kept in room B as compared with those kept in room A, though the temperatures of the two rooms did not differ appreciably. The age at which the first brood of young was produced was also greater in individuals from room A. As mentioned above the only obvious feature in which the conditions differed in the two rooms was in the amount of light the cultures received. This strongly suggests that light may be an important factor in maintaining a high reproductive rate; a conclusion which I have been able to confirm for Daphnia obtusa (see below). It is of interest that, judging from the form of the egg-production curves, the effect of lack of light is more marked on younger individuals, than it is on older ones. This effect of light and its possible ecological significance will be discussed more fully below.

The effect of crowding is less conspicuous, but is still well-marked, especially in view of the very sligh degree of crowding involved.

All three sets of observations showed a consistently lower total egg-production than the uncrowded. This appeared to be due entirely to a reduced reproductive rate, since the ages at which the first brood was produced did not differ significantly as between crowded and uncrowded cultures. Unfortunately the form of the egg-production curves is such that they cannot readily be analysed statistically; but there can be little doubt that the effect is real, especially in view of its consistency.

In order to understand the mechanisms of these effects on reproduction, the data must be further analysed, and I have done this in tables 6 and 7, and figures 3 to 5. Table 6 and figure 3 show the total number of completed adult instars plotted against time. Under all conditions this is clearly a simple linear regression. Thus it appears that the frequency of moulting, and hence the instar length, remain constant, at least during the earlier part of adult life. However, since at least four or five instars have been passed through before the end of the first adult instar, it is clear that the juvenile instars must be very considerably shorter than the adult instars, in agreement with the conclusions of previous workers. The frequency of moulting is very considerably greater at the higher temperature, but neither light nor crowding affect it significantly. Since the number of broods produced in a given time is greater at 27°C than at 18°C, the average number of young in each brood must be considerably less at the higher temperature. This is clearly shown in table 7 and figures 4 and 5.

The average egg-numbers are unfortunately exceedingly variable. This is partly due to inherent variability between individuals and partly due to variations in brood size from moult to moult. On the whole these do not follow any definite pattern and must be attributed to uncontrolled variables in the experiments. The most likely factor involved is the effects of temporary crowding due to the production of considerable numbers of young at an early time in the two-day observation period. Well over 100 young were sometimes produced during two days so that for short periods the cultures showed a considerable degree of crowding, far greater than that which was intentionally produced in the 'crowded' cultures. Thus there was a considerable degree of overlapping between the egg-numbers recorded under the various conditions, and to some extent this variability obscured the essential features of the action of the various factors on average egg-number. Nevertheless the main features of these actions are brought out by appropriate analysis. The egg-number of those individuals kept at 27°C is markedly lower than that of individuals kept under similar conditions at 18°C (Pooled means of crowded and uncrowded 8.56 at 27°C, and 15.64 at 18°C.) This effect of temperature accounts for the greater part of the large item appearing under 'rooms' in the analysis of variance, and is highly significant. The egg-number is also lower in the dark room at 17°C than it is in the light at 18°C but the effect is not very considerable in comparison with the large error.

The crowded cultures show lower egg-numbers than the uncrowded, but the analysis shows that this effect is just not sufficiently marked to be significant. It is, however, almost significant, and is actually quite large, but swamped by the very large error variance. In the light of this considerable random variation, and also of the very conspicuous and consistent effect on total egg-number, there can be no doubt that the effect is real. To establish a significant result would involve a very large experiment, which would have been too ambitious for a single worker to handle.

The interaction between 'rooms' and crowding is not very large, and is certainly not significant. It is almost entirely due to the greater effect of crowding in depressing the egg-numbers of the animals in room B as opposed to the two other sets of animals. There is no reason to believe that this effect is real, and even when the two low temperature series are analysed separately from the high temperature results it is still far from significant.

The depressing effect on reproduction shown by even the slight degree of crowding in my crowded cultures (1 animal to 16.67 ml.) supports the views of Banta, and Macarthur and Baillie, who maintain that for optimal conditions Cladocera should be kept at very low densities. Moreover my results establish that whatever the cause of reduction in egg-number it is not an effect of shortage of food, a possible factor in the results of previous workers. Higher degrees of crowding produce more marked effects on egg-number as Pratt (1943) showed. The fact that the effects of crowding begin to be felt at very low densities renders several possible mechanisms for the effect unlikely. It is not really feasible that at these low densities animals are prevented from obtaining adequate food supplies, by the mutual interference of their feeding currents. At higher densities such an effect might be important. At high densities constant collisions of animals may cause temporary cessation of feeding; but such collisions are too infrequent to be of any importance at a density of 6 animals to 100 ml. The number of individuals is also far too low to have appreciable effects on the oxygen tension of the culture water. Thus the effect of crowding is distinct from that of oxygen, though lack of oxygen also lowers egg-production. (Unpublished work of Miss E. Phear). Pratt's contention that the accumulation of deleterious metabolites depresses egg-production seems to be the only reasonable explanation of the facts. It must be noted however that the effective metabolites are not necessarily produced by the Daphnia themselves, but may result wholely or in part from the activities of the food-organism. To maintain an equivalent food-supply the concentration of this must be increased in the same proportion as the concentration of the Cladocera, and as is well-known high concentrations of algae may produce substances toxic or deleterious to other organisms (Lucas 1947). From my observations I am convinced that very high concentrations of <u>Chlorella</u> are deleterious to <u>Daphnia</u>, but this effect seems to be largely mechanical. The <u>Chlorella</u> clogs the limbs of <u>Daphnia</u> individuals, and also settles and reproduces on the carapaces of living individuals. These effects only occur however at concentrations considerably higher than those which I have used in my experiments. There is some indirect evidence that the main effect of crowding in this experiment was due to the Daphnia themselves. In subsequent experiments where cultures showing the same degree of crowding were fed with different quantities of <u>Chlorella</u>, the egg-number was always higher in those cultures receiving the most <u>Chlorella</u> (see below) even when this was considerably in excess of their requirements.

Throughout this experiment, under all conditions, there was some excess food left at the end of each two day period. One is tempted to assume from this that in all cases the animals received as much food as they could consume and utilize, as Pratt (1943) did in his experiments. This however was apparently not so. Though animals collected from the field usually have lower egg-numbers than the highest recorded in the experiment, much higher egg-numbers are occasionally met with. Again I have obtained considerably higher egg-numbers in individuals reared in the laboratory under good conditions, and the egg-numbers of the animals at a high food-level in experiment B (below) are also noticeably higher. The Daphnia magna used in this experiment were a different strain, being derived from the Wellcome Institute, and not from the College Botany Garden. This strain from the Wellcome Institute is usally regarded by the members of this department who have worked with it as showing low egg-numbers, so that there is no reason to suppose that the higher egg-numbers that I obtained were a consequence of using a more fertile strain, It thus seems highly probable that, under certain circumstances, Daphnias fail to consume all the food available, even when the total amount of food given is less than the maximum amount that can be utilized, under the same general conditions, but with a higher food supply.

Experiment B.

This experiment was actually conducted at a later date than experiment C. but since it corresponded closely in design to experiment A, it is most logically treated here. However the results of experiment C. led me to adopt slightly different experimental techniques to those used in experiment A.

The aim of the experiment was twofold. I wished to extend the conclusions concerning the effects of temperature on reproduction, derived from experiment A., by comparative observations on a number of species. I also wished to find out what, if any, were the interactions of temperature and food-supply in respect of reproduction. I would have liked to investigate the effects of light and crowding simultaneously with food and temperature, but such a comprehensive experiment would have been far too large for me to cope with, with the limited facilities available in a small laboratory. Similar considerations of time, labour, and available apparatus, limited the number of species which I could investigate in this way. I finally decided to consider three species only : *Daphnia magna*, the individuals of which were derived from a culture kept at high temperatures (28 - 30°C) in the Wellcome Institute: *Daphnia pulex*, the race investigated being one with a comparatively low thermal deathpoint from the Leg of Mutton Pond on Hampstead Heath (see above); and *Ceriodaphnia dubia*, a more or less lacustrine, summer species, with a somewhat southern distribution, the source of which was Regent's Park Lake.

The general experiment techniques and procedures used in this experiment were the same as those I have described in connection with experiment A., and I will only refer to differences in procedure here. Since it was clear from experiment C./ that light had a profound effect on reproduction at least during the earlier instars, all the experimental vessels used in this experiment were kept in darkness, the cultures only receiving light for the brief period in each 48 hrs./ when the culture medium was changed, and the food-supply renewed. A high temperature of 27°C was again maintained by means of a water-bath, and the low-temperature cultures were kept in a dark room with a fairly constant temperature of about

16°C. I originally intended to use 6°C as an additional temperature, but growth and reproduction were so slow at this temperature that the experiments had to be abandoned. *Daphnia pulex*, for instance, took over 21 days to reach maturity at this temperature. Since I was not concerned with investigating the effects of crowding, in this experiment, I chose the population density at which the experimental beakers were kept on grounds of convenience. The density chosen was 1 animal to 20 ml. Thus at each temperature and food-level I started the experiment with one 250 ml. beaker for each species, containing 200 ml. of culture medium, and 10 neonatae. With *Ceriodaphnia dubia* and *Daphnia pulex*, I was able to run the whole experiment in duplicate, but~~,~~ I was not able to do this with *Daphnia magna*, owing to shortage of available neonatae. The food-levels chosen were such that the highest provided more than sufficient food for all species under all conditions. I abandoned the method of standardization of *Chlorella* suspensions used in experiments A, and C., in favour of comparison of the suspension with a standard grey wedge, by means of an M.R.C. grey wedge photometer, using a number 2 filter. The *Chlorella* suspension was adjusted till on diluting 2 ml. to 12 ml. the resulting suspension gave a colorimeter reading within 3 divisions of 90. This method of standardization is very much quicker than the Nickel sulphate - Keiselguhr method and avoids most of its difficulties. The cultures kept at a high food level were given .5 ml of the undiluted suspension per individual. Those kept at a low food level were only given .1 ml. As in the previous experiments the cultures were fed every two days.

A difficulty that results from starting experiments with neonatae is that of distinguishing very young males from young females. For practical purposes their separation is not feasible at such an early stage. In consequence of this some of my experimental animals used for the low temperature experiments Ceriodaphnia dubia proved to be males. Unfortunately I did not discover this until the experiment was well under way. As it was not possible to repeat the experiment, since there was insufficient time available, I decided to continue with it unchanged. In counting the ecdyses I only counted those of females, the two sexes being easily recognizable by the form and structure of the carapace. However, I based feeding levels and population densities on the total number of individuals whether male or female. Deaths of both males and females were recorded.

A different complication occured in the low temperature Daphnia pulex experiments. A saprolegniaceous fungus, parasitic in the brood-pouch of the Daphnia, mainly on the eggs, suddenly appeared in the experimental cultures. The source of this fungus was not clear, but presumably it originated from a spore introduced with the lake-water. The fungus drastically reduced the egg-numbers of the individuals, and perhaps also increased the mortality rate. I had already obtained sufficient results to establish the rate of moulting and the egg-production of the species, under these experimental conditions, but I decided to continue the experiment, since it provided a unique opportunity of showing the effect of a parasite on reproduction in the Cladocera.

The results obtained in this series of experiments are shown in tables 8 to 13 and figures 6 and 7. The records below the horizontal line in the tables for Daphnia pulex at low temperatures are those obtained after the egg-parasite had become established. It was possible to follow Daphnia pulex and Ceriodaphnia dubia throughout life, though I have not recorded young and ecdyses for the last surviving individuals, since it was not possible to keep conditions constant with the small volumes of culture medium and food-suspension required. I recorded survival, however, since it was unlikely that the slight variations from standard conditions would affect this to any great extent. Shortage of time unfortunately prevented me from following the cultures of *Daphnia magna* throughout life in the same way. The figures for total numbers of instars, and for total egg-production have been corrected for deaths, as in experiment A.

As in the previous experiment the figures for total production of young in a given time are complex and not easy to interpret until they have been analysed into their constituents parts, and for this readon I prefer not to discuss them in detail. The two Daphnia species differ very strikingly from *Ceriodaphnia dubia* in the effect of high temperatures on their reproduction. It is very clear from the results that the optimum temperature for reproduction in these two species is considerably below 27°C, *Daphnia magna* being less adversely affected by this temperature than *Daphnia pulex*. On the other hand high temperatures are clearly favourable to *Ceriodaphnia dubia*.

The effect of the parasite on production of viable young is clearly shown by the falling off in production of ~~of the curve for total young in~~ *Daphnia pulex* at low temperatures (Table 9c). On the assumption that the rate of reproduction would continue at a similar level to that last recorded, an assumption which I believe to be justified, it is possible to form an estimate of the mean production of young by one individual throughout its life in the species where I have determined the mean length of life. Estimates obtained in this way for the well-fed individuals are for *Daphnia pulex* at 27° C, 3.2, and at 16° C, 25.5; for *Ceriodaphnia dubia* at 27° C, 65, and at 16° C, 58. The data are insufficient to determine the fertility of Daphnia magna in the same way, but it is clearly much greater than in the other two species. Probable figures are about 135 at 27° C and about 300 at 16° C. These figures may be compared with those given by Banta for his race of Daphnia longispina (see above). Whilst there are considerable differences between the species, the figures are all of the same order, and may be taken as typical of the Daphniidae. It must be realized however that conditions in nature are rarely so continuously favourable as in these laboratory cultures so that actual fertility of individuals in wild populations will usually be lower. The surprisingly rapid increases and decreases in population density shown by wild populations of many Daphniidae give the impression of high fertility, but these results show that this is not the case, the sudden changes in population levels being due rather to the high reproductive rate of individuals. The actual fertility is not exceptionally high being of the same order as that of many insects and small arachnids. Cladocera may be regarded as being semi-viviparous, and their fertility is appropriately intermediate between that of many marine species, with long larval histories, and that of forms with more highly developed viviparity or very large yolky eggs (e.g. Glossina morsitans, the tropical Bulimi).

Tables 10 and 13 and figure 6 show the frequency of moulting of the three species. As in experiment A the results indicate that the length of instars is constant throughout adult life. The results for Ceriodaphnia dubia at 27° C form a marked exception to this statement. In this species, under the conditions of this experiment, the regression line for total number of instars against time differs significantly from a linear regression. (It is possible to ascertain this, since the observations were conducted in duplicate.) The frequency of moulting increases throughout the earlier portion of adult life, though it appears to become constant in older individuals, that is to say the average instar length decreases with increasing age, during adult life. This result is in striking contrast to the increase in instar length with age claimed by Banta (1939) and Anderson and co-workers (1932, 1942). Banta had simultaneously measured size of brood in each instar, and the growth increment due to each instar. He attempted to show that these quantities were all intimately related, though the actual relations are, of course, complex. It is not quite clear from his discussion whether he considers instar length to depend on egg-production and growth, or, as seems more probable, that these last quantities are influenced by instar length. These correlations may well be real, but this further attempt to associate variations in the quantities with age, is only applicable to his own data. Since length of instar does not commonly increase with age as Banta thought, the whole of his theory needs re-investigating. Unfortunately I did not realise the importance of this discrepancy between my results and his and so I did not make any measurements of growth increments which would have made it possible for me to check fully whether or no his general hypothesis holds when instar length remains constant or decreases during adult life. The possibility that it may do so is suggested by the fact that in most of my cultures, though the egg-number varied from observation to observation, the variations followed no definite pattern. On the other hand there was a marked decrease in egg-number during the later life of Ceriodaphnia dubia, an observation which shows general agreement with Banta ideas.

Table 13 shows the regression coefficients for the ecdyses-time relation calculated on the basis of ten animals. For the high temperature records of Ceriodaphnia dubia only the later results, corresponding to the maximal moulting frequency, were used in calculating the regression coefficient. This method of expressing the data is the most natural, but for the purpose of comparison with the results of other workers I have, in Table 14, recast them in terms of mean length of instar. I have included in this table the results I obtained for Daphnia magna in experiment A, and also some results of previous workers. The three species I have investigated show slight differences amongst themselves in respect to frequency of moulting, and there is also a slight difference between the moulting frequencies of the two races of Daphnia magna. These differences between the species are however remarkably small, especially if the size range is taken into account. My results are also completely consistent with the majority of published results, and it is difficult to avoid the conclusion that length of instar is fixed to within quite narrow limits for the Daphnia section of the Daphniidae.

As was to be expected temperature has a profound effect on the frequency of moulting in all three species which I have investigated, the moults being considerably more frequent at the higher temperature. In table I have given the ratios for increase in moulting frequency for an interval of ten degrees, based on the data of this experiment and experiment A. All these ratios are of the same order and the slight differences are not readily correlated with differences in the ecology of the species. The ratio is greatest in Daphnia pulex, a species of fairly general occurence in summer and winter, and least in Ceriodaphnia dubia which is a summer form in England. As a species Daphnia magna is more common in summer than in winter, and this may be taken as corresponding with the intermediate value of the ratio, but it must be noted against this that the Wellcome Institute race has been living under constant high temperatures for a number of generations. It is not easy to see how a reduced effect of temperature on moulting frequency can be of any benefit to species which are normally found in summer rather than winter, and I do not wish to lay stress on this apparent correlation in these three species, since it may prove to be spurious if a greater number of species are examined. The ratios I have obtained between frequencies of moulting at temperatures differing from each other by 10° C may be compared with the similar ratios obtained by Brown (1929 b) for rate of growth in several species of the Cladocera. These ratios ranging from 2.39 for Moina macrocopa to 1.31 for Daphnia magna and 1.19 for D. pulex (986), are of the same order as my results, as might be expected since growth is so intimately associated with moulting in the Crustacea. Browns results indicate however that the increase in growth rate with rising temperature is greater for warm-water, than it is for cold water species. He considers this is an adaption to the normal temperature conditions under which the species live, but does not make it clear how the differences can be of benefit to their possessors. In this respect my results do not agree with those of Brown; but it must be born in mind that classification of species in relation to their occurence in nature must be somewhat arbitrary. If the three species which I have investigated are grouped according to spatial distribution, instead of according to seasonal occurence, then their order is reversed, and my observations fall into line with those of Brown. It may be that this is the correct arrangement, and the apparent correspondence with seasonal distribution an experimental accident. This can only be solved when more species have been investigated, but such a task will probably take several years.

My results, and those of Brown, both differ considerably from the figures obtained by Fox and his co-workers (1947-1949) for the effect of temperature on metabolism, as measured by oxygen consumption, in various marine invertebrates. These workers were able to show that animals were well adapted to the temperatures at which they lived, but the adaptation affected the rate of metabolism at all temperatures, animals adapted to low temperatures showed higher metabolic rates at their normal life temperatures than animals adapted to high temperatures. The actual increase in metabolic rate for a given rise in temperature did not show any clear correlation with the temperature of the normal habitat. It thus seems clear from a comparison of these results that the mechanisms of temperature adaptation are very different in the Cladocera from those found in marine invertebrates. These differences, as also the differences in thermal resistance (see above), may be associated with the often pronounced stenothermy of marine invertebrates, on the one hand, and the usual eurythermy of Cladocera, on the other.

Food supply has no effect on the frequency of moulting, either at high or low temperatures, the slight differences between the calculated regression coefficients for well-fed and poorly fed animals being quite insignificant. In this the action of food agrees with that of crowding and light. On the other hand Anderson and Jenkins (1942) believe that food shortage is associated with longer instars.

The age at which the first brood is produced, see table 13 , is affected by two processes, the frequency of moulting of the juvenile, and the age in instars at which the animals become mature. Banta showed that the last age was constant for his race of Daphnia longispina, but in other strains it may vary at least one instar (Anderson (1932), Anderson, Lumer, and Zupancic (1937), Anderson and Jenkins (1942). Frequency of moulting in the juvenile is presumably affected by environmental conditions in much the same manner as in the adult, but there is no reason to suppose that the effects are of exactly the same degree in each case. In general one would expect that the age of production of the first brood would be roughly correlated with the frequency of moulting,but that this correlation would be of a rather loose nature. This is in fact what I have observed. The first brood is always produced at an earlier age at high temperatures than at low temperatures, but the difference in days is not clearly assoicated with the effect of temperature on the frequency of moulting. Food supply does not normally affect the time at which the first brood is produced, but it has a marked affect on individuals of Daphnia magna at 27° C. This is comparable to, but even more marked than, the effect of light shown in experiment A. It appears that both shortage of food, and lack of light, may, in certain circumstances, delay the attainment of sexual maturity by one or more moults.

// From the ecological view-point, the results for egg-numbers are of more interest than any of the features so far mentioned. The total number of viable young produced per brood varies considerable from species to species, and with both temperature and food-supply; morevoer the effects of temperature and food-supply differ significantly as between species The three species differ significantly in egg-production, quite apart from the effects of temperature and food (tables 9, 11). The higher egg-numbers shown by *Daphnia magna* are perhaps connected with its large size, but size alone does not explain the differences, since if the specific egg-number were mainly dependent on size, that of *Ceriodaphnia dubia* would be expected to be far smaller than that of *Daphnia pulex.* In fact the species mean obtained for this species is slightly higher than that for *Daphnia pulex.* The strain of *Daphnia pulex,* which I have investigated in these experiments, appears to have an unusually low egg-number. Field-observations suggest that such strains are not uncommon and are genetically determined, but it is clearly not possible to test this by experiment except in a very few races.

Whilst both temperature and food supply affect the numbers of young per brood, the effect of the latter is the most striking and consistent. In all three species the average egg-number is lower in the poorly fed cultures. The effect is particularly striking for *Daphnia magna,* and least marked for *Ceriodaphnia dubia.* It seems fair to assume that this difference is correlated with differences in size of the three species, *Daphnia magna* being by far the largest, and *Ceriodaphnia dubia* the smallest. Rather surprisingly, the analysis of variance shows that there is not interaction between the effects of food-supply and the effects of temperature. Since there is also no third-order inter-action between food-supply, temperature and species, this means that food-supply and temperature act independently on egg-number. This is important in the interpretation of the effects of temperature.

The two Daphnia species agree with each other in that the egg-number is lower at 27° C than it is at 16° C. The effect is most striking for D. pulex which shows scarcely any egg-production at the higher temperature. A high proportion of the eggs produced by the individuals of this species were ephippial eggs, which, remaining unfertilised in the absence of males were resorbed. No ephippial reproduction occured at 16° C, nor was it observed in the other two species. Ceriodaphnia dubia by contrast with the other two species shows higher egg-numbers at 27° C than at 16° C. Though the two species of Daphnia are pond species, and therefore likely to encounter higher temperatures in the summer than Ceriodaphnia dubia they are species which occur throughout the year and reproduce freely in spring and autumn, whereas the lacustrine Ceriodaphnia dubia is definitely a summer form. In its reproductive behaviour it is clearly adapted to higher temperatures than the other two species. This adaptation is not correlated with an exceptionally high thermal resistance, the two races of Daphnia magna which I have investigated both being somewhat more resistant to high temperatures. Thus it seems that in this group thermal resistance is not necessarily correlated with other adaptations to temperature, and may be missleading if taken by itself. Since species of Daphnia reach an obviously greater size at low temperatures, than they do at high temperatures, and since this size difference is much less marked in the case of Ceriodaphnia dubia, it may be suggested that the lower egg-numbers of the Daphnia species at high temperatures are a consequence of the smaller size of the individuals. Some support for this idea comes from the work of Cheng (1944) who concluded that in the marine Polyphemidae, Evadne and Podon, the egg-number was to a great extent determined by the size of the individual. Unfortunately I did not realise that such a connection might exist before performing these experiments and so did not make records of the sizes attained by the individuals as well as of their average egg-numbers. However I did possess three sets of observations in which I had made simultaneous measurements of the sizes and egg-numbers of a number of individuals of two species of Daphnia (see table 1). These results indicate that egg-number is not dependent to any significant extent on individual size. It thus seems unlikely that the lower egg-numbers of the two species of Daphnia at high temperatures are a consequence of their reduced size. Another possible explanation of this reduction of egg-number at higher temperatures would be that the individuals were unable to obtain sufficient food to maintain their high egg-number and the increased metabolism consequent on the higher temperature. If this were so one would expect an interaction between the effects of food and temperature, since a sufficiently high food-supply would compensate for the increased demand due to higher metabolism. Since there is in fact no temperature-food interaction this explanation of the effect of high temperatures on egg-numbers must be abandoned. The available evidence suggests strongly that temperature acts directly on the activity of the gonad. Such a direct action would be consonant with the effect of more extreme temperatures in inducing the production of resting eggs, no matter how good other conditions may be.

The high egg-numbers which I have found in this experiment for well-fed individuals of D. magna are of great interest. They are quite comparable with those observed in very flourishing colonies in nature, and much higher than most egg-numbers of laboratory animals, recorded in the literature. Particularly they are higher than those recorded by most American workers who have used Banta's culture medium. Banta himself was able to obtain some high egg-numbers with this medium, using very low population densities (as 10 to 33 for *D. longispina*) but most of the egg-numbers recorded by workers using bacterial culture mediums are low (e.g. Anderson, 1933, 10 to 17, McArthur and Baillie C 6 for *D. magna*) On the other hand Pratt (1943) records quite high egg-numbers 104.5 at 18°C and 53.9 at 25°C at densities of one animal to 50 ml; 10.7 at 18°C with 1 animal per 2 ml, and 26.7 at 25°C with one animal per 10 ml., for *D. magna* using *Chlorella*, as food-supply. These results confirm the theory that the principal food of most species of *Daphnia* is provided by small algae (see below.) It is of interest in this connection that *D.longispina* s.s. appears from other evidence to be less strictly an algal feeder than most species of *Daphnia*. Banta found that in *D. longispina* the egg-number increased gradually during the earlier instars to a high maximum and then showed some falling off in old individuals, and this seems to be a rather general opinion. Some of my animals did show such a pattern, but in the majority it was not possible to detect any long-term trends in egg-production. It is clear that this effect of age on egg-number is not of any great importance since it is so easily swamped by other variations.

The poorly fed clone of *Daphnia magna* at 27°C besides showing a low egg-number did not attain to such a large size as those in the well-fed culture. ~~The average size of our survivors from each culture was~~ Such dwarfing of starved animals has been noted by several authors, including Ingle (1933, 1934, 1935, 1936); Ingle, Wood and Banta (1937), showed that if such individuals were subsequently given ample food, they rapidly attained a normal size.

The effect of the saprolegniaceous egg-fungus, which has been called 'brood-pouch disease' on the production of viable young is very striking as shown in the results for D. pulex. The viable young produced per brood in each instar were reduced to a small fraction of those produced before the onset of parasitisation. However a few young manage to develop despite the presence of the fungus. This reduction in the number of viable young produced is a result of the killing of eggs after they have been layed, and not of a reduction in the number of eggs layed, as is shown by the occurence of many dead eggs in the exuviae.

Analysis of the data for longevity shows that the two species concerned differ in absolute longevity, but are affected to the same extent by temperature, within the limits of error of the experiment. The effect of temperature is of course to reduce the length of life. The extent of this reduction is consistent with the suggestion that it is mainly caused by a decrease in the duration of adult instars, so that the individuals attain to the same age as measured by the number of instars passed through at each temperature. ~~These mean survivals in terms of instars are~~ Within wide limits ~~and~~ food has no effect on survival and there are not significant species-food or food-temperature interactions. This last conclusion is in sharp contrast to the results of Dunham (1938) who found that animals with alternate periods of semi-starvation and abundant feeding had shortened life-spans.

Experiment C.

Since from the results of ExperimentA light appeared to have important effects on egg-number, I decided to test this experimentally.

The experiment was performed at room-temperature. 15 beakers were set up each containing three neonatae of Daphnia obtusa in 150ml. of water. Daphnia obtusa was chosen for experiment, solely because it was the only species available at the time. 5 of these vessels were kept continually in darkness, except for the short exposure to dim light, necessary in changing the culture medium and counting the young. 5 were exposed to the light of a fluorescent strip for 2 hrs. in every 24 hours and 5 were similarly exposed for 8 hours in every 24 hours.

The general technique of the experiment was the same as in experiment A., and the method of standardising the feeding, as also the amount of food given per individual was also the same. Fortunately it proved to be possible to assign the young produced to definite instars since the times of moulting were reasonably synchronous for all individuals. The experiment was continued until all individuals had passed through four complete adult instars. Numbers of young produced were determined as in previous experiments and dividing these by three gave the average egg-number. In vessel ~~five~~ 5 of the 0 light series, one individual was accidentally killed before reaching maturity, so that only two individuals from this vessel were available for determinations.

The average egg-numbers obtained are given in table 15. The average egg-number is lowest in the 0 light series, slightly higher in the 2 hours light series and much greater in the 8 hours light series. The analysis of these results shows that this effect of light is highly significant. The experiments thus clearly establishes that the presence of light increases egg-number in Daphnia, and that the degree of the effect is in some way dependent on the length of time to which the animals are exposed to light during each day. The figures also show that the relation between the number of hours exposure to light and the increase in egg-number is not a simple linear one, but the three points are not sufficient to determine the form of the regression. The effect was dependent on light, and not a consequence of variations in oxygen, since all vessels had similar oxygen tensions.

An incidental observation of interest in this experiment is the occurence of significant differences in egg-numbers between successive instars, these variations not showing any obvious trend. As noted above they possibly represent temporary crowding effects. In the other experiments described here it was not possible to treat the instars separately, so that the variations between instars were lost in the general error variance, and were probably partly responsible for its high value. There was no difference in the effect of light on the various instars.

After performing this experiment I came across the paper by Schultz (1928) on the effect of light on Daphnia. He had concluded that darkness causes a decrease in egg-numbers but an increase in size of individuals of Daphnia. As far as egg-number is concerned my results thus confirm this. Unfortunately, as I have noted above his paper is so vague, and contains so many inaccuracies and faulty deductions, that his work has been discredited or ignored by almost all subsequent workers. My results are thus useful as confirming the part of his work dealing with the effect of light on reproduction in Cladocera.

General discussion.

The conclusions from this whole series of experiments can be summarised as follows.

1. The fertility of *Cladocera* is low as compared with most invertebrates, as one would expect from the method of development of the young. The rate of reproduction is, on the other hand, very high.

2. Fertility depends on the frequency of moulting of the adult, the average egg-number, the age at which maturity is attained, and the length of life. All these are affected by temperature, in all species; but food-supply, light, and degree of crowding only affect egg-number, and sometimes, the age at which the animals became mature.

3. Instar lengths are of the same order throughout the Daphnia group of genera, and are affected to more or less the same extent by temperature changes. There are slight differences between the species in this respect which may be connected with the ecology of the species concerned, though this is not certain. The adaptation, if real, is of an entirely difference nature to those shown by marine invertebrates in respect to their metabolism.

4. The temperature for maximum egg-number differs in different species. These differences are probably correlated with the seasonal occurence of the species but show no obvious assoication with spatial distribution, or with the specific lethal temperatures.

5. Shortage of food, absence of light, and increased crowding all diminish the average egg-number, though they are not equally effective in this. These factors show no interaction with temperature, which indicates that, in those species where the egg-number is reduced by high temperatures, the effect of temperature is not mediated through shortage of food, caused by increased metabolism. The effect of food-shortage is less marked in some species than in others, and its degree is possible dependent, at least

in part, on the size of the individuals.

6. The saprolegniaceous egg fungus, 'brood-pouch disease', causes a marked reduction in the number of viable young produced, this being due to the death of eggs subsequent to laying. It does not appear to affect the frequency of moulting.

7. The age at which maturity is reached depends on several factors. It appears to depend mainly on temperature, but it <u>may</u> be considerably delayed by shortage of food or absence of light. This delay is probably due to a postponement of maturity for one or more instars.

8. Longevity is distinctly affected by temperature, the length of life being much reduced at higher temperatures, as noted by previous workers. Longevity also differs from species to species, as does the effect of increased temperature on longevity. Within wide limits, food-supply appears to be without effect. It is probable that, except at high temperatures shortening of life is dependent on shortening of the length of instars, the average age attained in instars being constant.

9. Egg-number and frequency of moulting may vary progressively during adult life, but often no such variation can be detected. In some cases variations occur which are exactly the opposite of those reported by Banta.

It is clear from these results that the actual effect of environmental conditions on the reproduction of Daphniidae must be complex, and it can be expected that some difficulty may be found in discovering absolute correlations between the distribution of a species, and its behaviour in regard to any one simple physical factor. Nevertheless, the differences in behaviour of species in respect to temperature are of a sufficiently high order for this to be a major factor in their ecology.

Its exact significance can of course only be determined when these reproduction studies are extended to a larger number of species. It may be noted that since reproduction inevitably increases population density, which will reduce the average egg-number of the population, the optimal temperatures and food-levels for fertility in nature may differ considerably from those found in the laboratory under conditions of more or less constant population density. It is also possible that the effect of these factors may differ according to the presence or absence of nearly related species, since presumably a crowding effect may be induced in a sparse population of a species by the abundance in the same locality of a nearly related species. In these circumstances it is not surprising that it is only occasionally possible to show from observations of natural populations that the seasonal occurences of some of their component species are dependent on temperature. Similar considerations apply to a less extent to the effect of food-supply, and the often noted difficulty which workers on plankton have found in correlating the occurence in numbers of zooplanktonts with algal abundance is not surprising. Indeed if the main food of Cladocera is provided by nannoplankton Algae then a strict correlation between the abundance of these two groups of organisms is not to be expected, though a general correlation should be shown if both abundance and egg-number of the Cladocera are considered.

The depressing of reproduction by darkness may be connected with a rather striking feature of Cladoceran distribution, the almost complete absence of these organisms from caves and deep wells. It must be noted however that the inability of most Cladocera to live in streams which show any appreciable rate of flow, would also tend to exclude them from the subterranean fauna, by preventing their entry, except in very special situations.

As I have noted above certain authors have used egg-number as a criterion of good nutrition. Provided that its limitations are clearly realized, this procedure appears to be justified. For populations under otherwise similar conditions a lower egg-number probably indicates a poorer food-supply, provided that the population densities are reasonably similar. All that can reasonably be stated of populations living under dissimilar conditions is that those with lower egg-numbers are living under conditions that are in some way less favourable to the species, than are the conditions under which those with higher egg-numbers are living. Even this vague conclusion is unsafe when only two populations are compared, since the differences in egg-number may be due to intrinsic differences in fertility. Since such intrinsic differences are presumably distributed at random in respect to environmental factors, they may be ignored when numbers of populations are examined. The use of egg-number in association with population density as a criterion of adequate food-supply is justified when numbers of observations derived from populations living under similar conditions in respect to one environmental factor or set of factors, are considered together, provided that the populations show a random distribution in respect to the other factors which influence egg-number. In this situation effects due to irrelevant factors cancel each other out. Such observations can be used to determine the relative values of different substances and organisms as food for Cladocera, on the basis of their occurence, abundance, and fertility. In My work on the food of Cladocera I have made this limited use of egg-number (see below.)

The conclusions which I have reached in this work, though based only on the genera Daphnia and Ceriodaphnia are probably applicable to all calyptomerous Cladocera in which the egg-number varies with environmental conditions, that is to the families Sididae, Holopediidae, Daphniidae, Bosminidae, Macrothricidae, and to the Eurycercinae. They clearly cannot strictly apply to the Chydorinae, and it is unsafe to extend them to cover the gymnomerous families.

The effects of crowding, light, and food-supply on reproduction, show such a marked general similarity that it seems possible that they all depend ultimately on the amount of food consumed, though direct action of excretory products or light on gonadic activity cannot be dismissed. Miss Phear (unpublished results) has shown by means of observing the rate at which Daphnia remove suspensions of graphite from solution, and also from direct observation of the frequency of limbbeat, that the rate of feeding was reduced at low oxygen tensions. It is possible that lack of light and crowding have similar effects, but the experimental difficulties involved in determining this have so far prevented me from checking the possibility. It is unlikely that the effect of temperature on egg-number is of this nature, since as noted above, one would expect in that event to find some temperature-food interaction.

Food and distribution.

In the last section I discussed the effect of the quantity of available food on reproduction. The amount of food available is clearly of importance in Cladoceran ecology, but its quality i.e. the type of food available may also be of importance. A considerable amount of work has been done on the food and feeding of Cladocera, though most workers have been almost solely concerned with planktonic or at least open water forms, the bottom living and weed-dwelling forms having been largely ignored. It is well-known that the Cladocera fall into two clearly defined groups on the basis of general morphology and feeding mechanisms. The gymnomerous species of the families Polyphemidae and Leptodoridae, with prehensile limbs, not enclosed in the carapace, can only be raptatory feeders. These two families contain only four freshwater species, though they include many marine species, and all except Polyphemus pediculus are planktonic. Bythotrephes and Leptodora are also of large size, extremely transparant and very difficult to examine without damage. Perhaps for these reasons little seems to be known about the food and feeding of members of these two families. It seems to be generally assumed that they are predators, though, as has often been pointed out, their weak mandibles must preclude them from eating any but the feeblest prey. I have not concerned myself much with these species, since ecologically they can scarcely be considered as belonging to the same group as the more 'normal' Cladocera. I have however made a few observations on the planktonic forms, and a considerable number of observations on Polyphemus pediculus. It is virtually impossible to determine the food of Bythotrephes and Leptodora by direct observation; the gut of the former usually proves to be empty when examined, though it may sometimes contain a few small unidentifiable particles, and I have never found any gut-contents in Leptodora. These observations, which are in line with usual experience are not incompatible with the theory that these species are predatory, but they do not give it any particular support. However I was fortunate enough to observe an individual of Leptodora in the act of seizing and securing a small individual of *Ceriodaphnia.* The captured animal was passed towards the mouth of the *Leptodora*, which appeared to attempt to hold or pierce it with its mandibles. Unfortunately owing to the confined space of the compressorium in which I had placed the *Leptodora* for convenience in observation, these operations were not successful, so that I could not follow the process of feeding. The observation proves that *Leptodora* is capable of capturing animals of quite considerable relative size. There is thus little doubt that *Leptodora* is predatory, and, in the absence of evidence to the contrary one can assume that *Bythotrephes*, which has very similarly modified limbs, is also a predator. On the other hand, my observations of gut-contents show clearly that *Polyphemus* is not a predator. I have seen several hundred individuals of this species and, with the exception of a few with empty guts, they have always had their guts packed with detritus, which was obviously of vegetable origin. In fact the food of *Polyphemus* does not differ appreciably from that of many other littoral Cladocera.

The Calyptomerous Cladocera, in which the limbs are almost or completely enclosed by the carapace, cannot possibly be raptatory feeders. The feeding mechanisms of these forms, which comprise almost all the freshwater Cladocera, have been investigated by a large number of workers including; Cannon (1933), Storch (1922,1924) Eriksson (1934), Graf (1930), Franke (1925) and Lochhead (1936). These authors differ violently on details of the feeding mechanism, but are largely agreed in regard to its main features. The most useful account is that of Eriksson (1934). From Erikkson's account it appears that there are three principal types of feeding mechanism in the group. It is well known that the Anomopoda show a more specialized mechanism that the Ctenopoda. In the latter group all the limbs, except the last are similar in structure and possess filtratory' setae, and it is the metachronal beating of these limbs which creates the feeding current. Almost all authors are agreed that the filtratory setae remove particles of food from the water, which fall into the ventral food-groove. They may then be rejected by the post-abdomen, or in some way passed forwards to the mouth. In regard to this latter part of the mechanism the various authors are in violent disagreement. The more specialised feeding mechanisms of the Anomopoda are of two very distinct types which represent a fundamental cleavage within the tribe. The most familiar is that described by Cannon (1933) and Storch (1922, 1924) for *Daphnia*, in which the principal feeding limbs are the third and fourth pairs, which are very similar in structure and have equally spaced' filtratory' setae. In these forms the first limb is always very small. This type of feeding apparatus is confined to the Daphnidae. In the other families; the Bosminidae, Macrothricidae, and Chydoridae the limb-structure and feeding mechanism are entirely different. The principal feeding limbs in these families are the second and third and the 'Filtratory' setae on the two limbs show very different spacings, those on the third limb being much more closely set than those on the second limb. Eriksson interprets these as coarse and fine filters but his evidence is purely morphological. The limbs posterior to the third limb are remarkable for their large exopodites. Th~~is~~e first limb in all these families is a very large stout prehensile one, bearing no resemblance to a phyllopodium. It is bend backwards partly covering the second limb, and its tip may often, as in *Chydorus sphaericus* slightly protrude from the carapace. As Eriksson has shown, the limb-structure and the direction of the feeding currents in Ilyocryptus sordidus, differs considerably from the usual chydoriform pattern. Eriksson regards it as belonging to a fourth type, but this view seems to be exaggerated. Judging from Eriksson's figures, and my own observations, its limb-structure is merely that of a macrothricid, highly modified in accordance with the burrowing habits of the animal. It may be noted that Leydigia shows some comparable, but much less extensive modifications. There certainly seems to be no reason for removing Ilyocryptus from the Macrothricidae on the grounds of limb-structure alone, though others of its may peculiar anatomical features might possibly justify such action.

Almost all workers on feeding mechanisms seem to be agreed that the so-called filtratory setae really do filter particles from the water, and thus the Cladocera can be correctly described as filter feeders. Examination of the evidence shows that it is by no means conclusive, and consists almost entirely of deductions from morphology, there being little or no direct evidence for such filtration. Woltereck (1928) does indeed state that he has observed a seasonal change in the closeness of the filtratory setae of a race of Daphnia longispina which was correlated with a change in size of the most abundant available manoplankton algae. This would appear to be good evidence in favour of the filtration hypothesis, but he gives no details of other variations in conditions or of the Daphnia. Thus the variation in setation of the third and fourth limbs may have been due to other factors, including the size of the individuals. As I shall show below, my observations make it doubtful that actual filter-feeding is the only, or indeed the principal mode of feeding, in many species though these could usually be described as vortex feeders. A few authors in the past have noted features which do not entirely agree with the filter-feeding hypothesis, though they have not abandoned it. Thus Lochhead in his study of the feeding mechanism of Penilia avirostris notes that the vast majority of the food-particles never even approach the 'filtratory' setae, but are drawn directly into the ventral food-grove, an observation that I have been able to confirm for Sida crystallina. Berg (1929) has noted the habit of Chydorus sphaerious and Anchistropus emarginatus of clinging to algal filaments by the ventral surface, and has suggested that they feed on small particles of food which they dislodge from this substrate, a method of feeding which can scarcely be called true filter-feeding; the bottom grubbing of various Daphnia species and especially Daphnia magna which has been noted by Wesenberg-Lund (1926), is also somewhat difficult to fit in to the filter-feeding hypothesis.

Regarding the actual nature of the food of Cladocera there is even less agreement. In this field perhaps more than any other, workers have suffered from the tendency to generalise too hastily on the basis of one or a few species, and also from the tendency to interpret results solely in the light of preconceived hypotheses. For this latter reason the opinions of many workers, as for instance of Woltereck (1928) are somewhat suspect. Another important limitation to the value of the published work is that almost all of it has been concerned with planktonic species or members of the genus Daphnia, which, even when they occur in small ponds are from the behavioural point of view, more akin to planktonic species than they are to the vast majority of non-planktonic Cladocera.

It seems now to have been established beyond question that the food of Cladocera is mainly particulate, and moreover consists of particles which are non-colloidal. Pütter (1909, 1919) advanced the theory that the dissolved organic matter was an important source of food for planktonic organisms. He maintained that if this were not so then it was impossible to account for the observed numbers of zooplankton animals. This theory was advanced however, before the discovery of the abundance of the minute nannoplankton and nannotripton. Since then the theory has been largely discredited. Krogh (1931) subjected it to an exhaustive criticism and shoed that it was mainly founded on faulty observational grounds. He concluded that there was no evidence whatsoever that dissolved organic matter was ever an important source of food for aquatic metazoa. Nevertheless some authors as Macan and Worthington (1951) think that the theory is not fully disproved. As far as the Cladocera are concerned the theory has been completely disproved by the experimental work of Gellis and Clarke (1935). They showed that Cladocera starved to death as quickly in solutions of organic matter as they did in pure mineral solutions. They further showed that colloidal matter, which had been previously looked upon as a source of food of Cladocera, was not important by itself. It could provide a certain amount of food, since the animals remained alive, but they did not grow or reproduce.

What sort of particles provide the main food of Cladocera is much less clear. Workers are divided into three main schools in their opinions; those who like Naumann (1918, 1921), and Weissman (1877), consider that the principal food of Cladocera is provided by detritus, and particularly by the minute nannotripton; those who like Woltereck (1908, 1928), Storch (1925), Pacaud (1939), and Lefèvre (1942) consider that they are mainly phytophagous, feeding on small algae; and those who like Banta (1937, 1939), and Stuart etal (1931) seem to consider that the Daphniidae at least are principally bacterial feeders. These differences of opinion are no doubt partly due to the difficulty of determining the real source of food, but are I think mainly due to real differences between species.

That many planktonic Cladocera are algal feeders seems to be generally agreed. Even Naumann (1914) has noted that Cyclotella is often consumed and digested by Daphnia and Bosmina. Woltereck (1926) showed that whilst he could rear planktonic Cladocera satisfactorily on nannoplanktonic algae, they starved and died when fed with detritus, protozoa, or bacteria. Wagler (1925) concluded that planktonic Cladocera fed mainly on algae, but decided that littoral and small pond forms such as Daphnia magna and Daphnia pulex were mainly detritus feeders. On the other hand Banta has successfully reared Daphnia longispina through many years on bacterial media.

There is considerable doubt as to which algae, if any provide the best food for Cladocera. Birge (1897) records planktonic Cladocera feeding on large blue-green algae; but such observations have not been confirmed by subsequent workers, and it appears to be generally agreed that the larger algae can be excluded from consideration as a source of food for planktonic Cladocera (see Woltereck 1926, Berg and Nygaard 1929). The statements in the literature would suggest indeed that this was true of all Cladocera, but, this is not so, as is obvious when the gut contents of some of the littoral species are examined. Some authors as Rylov (1935) and Naumann (1917,1918) consider that small coccoid Algae, such as Scenedesmus and Ankistrodesmus cannot be used as food by Cladocera, and Wagler considers that these two algae are actually deleterious, because of their spinous projections.

Storch on the other hand, finds that they are a very good food for Cladocera. Woltereck (1928) concludes that the evidence suggests that the principal food-organisms of the planktonic Cladocera are the minute nannoplanktonic flagellates, and this seems to be born out by the complete lack of correlation between the productivities of waters, as determined by the ordinary phytoplankton, on the one hand, and the zooplankton on the other. A few recent authors have made serious attempts to resolve these difficulties by carefully investigating the food of a number of species of Cladocera.

Pacaud (1939) studied the food of a number of small-pond Daphniidae by a combination of various techniques. He observed the rates at which the species cleared different suspensions of living and dead material, examined the gut-contents of various species, and noted the abundance of species in relation to the algae present. He concludes that *Daphnia magna*, *Daphnia pulex*, *Ceriodaphnia pulchella*, *Ceriodaphnia megalops*, *Simocephalus vetulus*, *Moina brachiata* and *Moina rectirostris* are mainly dependent on minute, delicate flagellates for their food. He admits that *Daphnia* and *Moina* may survive for long periods in the absence of an abundance of such flagellates, by feeding on tripton and bacteria, but notes that the populations are then anything but flourishing. He suggests that for such forms as *Leydigia* and *Macrothrix* vegetable debris may be more important as a source of food, by reason of its greater abundance.

Pacaud's conclusions regarding the food of Moina species, may be contrasted with the results of Stuart, Macpherson, and Cooper (1931). These authors found that populations of *Moina macrocopa* flourished when fed with living Bacteria, but could not survive on a diet of dead bacteria, even when these were freshly killed. They also found that some Bacteria were unsuitable as food, and a few were even poisonous.

Lefèvre (1942) fed *Daphnia magna* and *Daphnia pulex* on cultures of of a number of species of small algae. He concluded that whilst many were excellent as food, others were very poor. He decided that for an alga to be a good food for these species it must be rather small; must have a delicate cell membrane; and must tend to remain in suspension; but must not be too powerful a swimmer. He noted that the two species differed somewhat in their powers of catching and digesting algae. Most striking was his proof that some species of *Scenedesmus* and of *Ankistrodesmus* consituted an excellent source of food, though other species of *Scenedesmus* only gave rise to moderate cultures. Margalef (1948) has, in the course of a general study of the food of aquatic invertebrates, recorded the gut contents of a number of species of Cladocera. His records emphasise the variety of substances which may be consumed by a single species, for instance he records from *Daphnia magna*, the filamentous alga *Tribomema*, diatoms, conidia, fungi, sand and fine detritus. Unfortunately he does not indicate the relative quantities of the substances he records, or how far they appeared to be digested, so that it is not possible from his records to decide whether or no the majority of species are algal or detritus feeders. The general impression from his records is that whilst certain species, such as *Ceriodaphnia pulchellas* are predominantly algal feeders, others such as *Alona affinis* must feed entirely on detritus.

In investigating this problem I decided to adopt two different procedures, to investigate the gut-contents of a number of species, and to investigate the distribution in the field, of Cladocera, in respect to the abundance or scarcity of the various possible sources of food. If these two sets of observations showed a good generaly agreement, then it could be presumed that the conclusions derived from them were at least reasonably sound.

Examination of gut-contents.

The vast majority of Cladocera are small and reasonably transparent so that it is possible to see the gut-contents clearly when an animal confined in a compressorium is examined under the microscope. For such species dissecting out the gut-contents is not only unnecessary but undesirable. For the larger and the more opaque species I found some dissection to be necessary though I substituted it wherever possible by direct observation. I found that the simplest and best method of obtaining the gut-contents for examination was by gently compressing an individual under the cover slip of a compressorium. If this is done carefully it is possible in about a fifth of the individuals of most species to cause a complete extrusion of the gut contents which retain their relative positions undisturbed. Thus it is possible to compare the materials in the anterior and posterior regions of the gut. In a few species it was not possible to obtain such an extrusion of the gut-contents, this being particularly the case with many Chydoridae, because of the coiling of the gut. In such cases other methods of dissection had to be tried.

The animals on which these observations were made were collected in the field in the normal manner. Immediately on arriving back in the laboratory I transferred them to petri dishes containing clean water, and examined their gut-contents as soon as possible. These precautions were necessary since it was very likely that in the absence of their proper food-supply animals would feed on whatever food was available to them in the collections. Observations on such individuals would be just as valuable in deciding the normal food of the species, as would observations on the food of concentration camp inmates, in determining the normal food of human beings.

Unfortunately the results which I obtained do not lend themselves to concise tabulation, so I have given an extended summary of them in appendix 1.

In considering these results it is necessary to treat the non-plankboare and planktonic species separately. In the latter group I include the pond Daphnias and *Moina* for reasons given above.

It is clear that the non-planktonic species fall readily into two groups on the basis of their gut-contents, the only conspicuous exception, being *Chydorus sphaericus.* These two food-groups a and b, are characterised by gut-contents which consist mainly of algae, or mainly of vegetable detritus, respectively. I found no evidence ~~in~~ that any species ~~of~~ was primarily a bacterial feeder. ~~extensive bacterial feeding.~~ The principal algal feeders are *Sida crystallina*, *Ceriodaphnia reticulata*, *Simocephalus exspinosus*, *Simocephalus serrulatus*, *Scapholeberis mucronata*, *Ilyocryptus sordidus*, *Macrothrix laticornis*, ~~*Echinisca*~~ Macrothrix *tenuicornis*, *Lathonura rectirostris*, ~~*Peracantha*~~ Pleuroxus *truncatus* and perhaps *Alona rectangula*.

Acantholeberis curvirostris is probably mainly an algal feeder though the records show that it also takes a considerable quantity of detritus. The forms which feed principally on detritus comprise, *Latona setifera* *Ceriodaphnia megalops*, *Simocephalus vetulus*, *Strebocerus serricaudatus*, *Eurycercus lamellatus*, all the Chydorinae examined, except the two species previously menttioned and *Chydorus sphaericus*, and *Polyphemus pediculus.* It must be realised that the extent to which the food of a species is limited to either algae or detritus varies considerably. Thus whilst *Eurycerous lamellatus* and *Leydigia leydigi* are strict detritus feeders, only consuming such algae as are inevitable owing to the rather poor selective mechanism, species such as *Ceriodaphnia megalops*, *Simocephalus vetulus*, and *Alona affinis*, are less discriminating. Again *Sida crystallina*, and *Ilyocryptus sordidus*, are strict algal feeders, but such species as *Ceriodaphnia reticulta*, and *Scapholeberis mucronata* may on occassion take considerbale amounts of debris.

Chydorus sphaericus does not fit readily into this classification, and my imprsssion is that it eats whatever food happens to be available at the moment, irrespective of its nature.

Limitations of food-supply other than the broad one just dealt with are less easy to determine. For most species the gut-contents represent a fair cross-section ~~for~~ of the algae or detritus present in the habitat which lie below the maximum size of particles that the species can consume. This limitation as to size clearly has no relation to the coarseness of other wise of the filtratory setae. In many species the normal size of the particles consumed is far above the distance between adjacent 'Filtratory' setae, and the largest particles consumed are often so large that it is not feasible to think of them being filtered out of the water. This is particularly striking in the case of *Sida crystallina* whose main food concists of algae of considerable size, such as large desmids, large diatoms, and Botryococcus. The species may also consume algal filaments of considerable length and diameter. *Eurycercus lamellatus* may consume such unwieldy objects as considerable sized fragments of cladoceran limbs. The general impression given by these observations is that the size of particles consumed is closely connected with the size of the species, the larger species feeding principally on larger Algae or detritus fragments. The largest particles recorded for each species are mostly those which have a breadth equal to the internal diameter of the mid-gut. Thus the upper size limit for particles consumed is probably determined by the animals swallowing capacity. The lower size limit is fixed by the size of the mesh formed by the seta and setules of the filtratory limbs. However this is a minimal size, and my impression from the examination of the gut-contents is that it is rarely reached in most species. In such species as Sida crystallina such small particles are certainly not important.

If a substance is to be a satisfactory source of food it must be digested as well as ingested. As the records show, species differ widely in their digestive capacities. These can best be examined in regard to the digestion of Algae, since the stages of digestion are much more clearly recognizable in these than they are for detritus. A difficulty is that dead algae may be present in the habitat in large numbers. This can be overcome by three types of observation. The percentage of dead algae in the habitat may be noted, in most habitats, though not in all it is found to be insufficient to affect seriously conclusions based on gut-contents. The algae at the front of the gut may be compared with those more posteriorly. If an alga which is represented in the anterior portion of the gut, largely by more or less intact individuals, is mainly represented posteriorly by fragmentary remains; or (provided it is fairly uniformly distributed in the habitat) is completely absent posteriorly, then it can safely be said that the majority of individuals of this alga have been digested. Similarly if two individuals cladocera from the same habitat differ considerably in the percentages of an alga in their guts which are dead, then, provided that both species are algal, or both species are detritus feeders, their digestive powers in respect to this Alga can safely be said to be different. If as sometimes happens, a larger proportion of undigested remains of an Alga appear in the gut of a detritus feeder than in the gut of an Algal feeder from the same habitat, it is clear that the detritus feeder is less capable of digesting this Alga than the algal feeder.

Bearing all these qualifications in mind, my results show that there is considerable variation between the different species in their digestive powers. On the whole the detrius feeders seem less efficient at digesting Algae than the algal feeders, which is as one would expect. It seems also that the larger a species is the more likely it is to have an efficient digestive mechanism. The digestibility of the Algae consumed also varies considerably. On the whole my observations agree with those of Lefèvre, who concluded that thinner walled species were more easily digested than those with thicker walls. However Desmids and Diatoms form striking exceptions to this rule. If these are eaten at all they are mostly efficiently digested, sometimes much more so than apparently naked flagellates. A probable explanation of this apparent anomaly is that in both groups the cell wall is pierced by openings of comparatively large size, which would thus enable the digestive enzymes of the Cladoceran to penetrate with comparative ease. Large mucuous sheaths on the other hand definitely hinder digestion, so that such forms as <u>Sphaerocystis</u> are scarcely ever digested. It is probably the occurence of such sheaths which hinders the digestion of many of the small coccoid Chlorophyceae which one would expect to be highly digestible. Certain portions of the algal cell seem never to be digested by any species. Outstanding are cellulose cell-walls. The remains of algae in which these walls are distinctive, as for instance *Chodatella* and many of the Desmids, retain their form so well that they can readily be identified as far as the species. The walls of Diatoms also remain undigested. Plastids are digested but chlorophyll itself appears to be indigestible. At any rate it accumulates and becomes highly concentrated in the fluid of the gut, often giving it a characteristic green colour.

It was stated above, that most species of Cladocera seem to feed indiscriminately on particles of the right size apart from showing a preference for either Algae or detritus. It might be thought that feeding is really indiscriminate and that the apparent preference for algae or detritus was due to the failure of the species to survive where whichever constitutes the main food is scarce. Though this may be partly true it does not fully explain the facts and one is forced to postulate some selective feeding, though this may be largely due to selection of feeding site, rather than to selective rejection of food. When I have examined species from habitats in which both algae and detritus were abundant, they have retained their algal or detritus feeding tendencies. Only in a very few instances when the preferred food was extremely scarce in comparison with the alternative food-source have I found individuals with markedly abnormal gut-contents. In *Sida crystallina* and *Ilyocryptus sordidus* this selective feeding is very clear. The former is not merely an Algal feeder but it also shows marked preferences for certain types of algae, when these are available, and particularly for Diatoms and Desmids. In one case I found a population of this species at Borran's Field, Windermere, in which the guts of many individuals were choked with partially digested remains of Gonatozygon brébissonii, though I could not find a single specimen of this rare alga in any of my collections from the locality. Thus this species is certainly selective in its feeding. Ilyocryptus sordidus lives almost completely buried in fine mud, often associated with the detritus feeder Leydigia, the gut however, hardly ever contains any mud, and rarely any detritus, but is usually completely packed with small Algae, drawn in from the mud-surface. This is of course largely rendered possible by the peculiar structure of its thoracic limbs (see Erikson, 1934).

It is much more difficult to interpret the records for planktonic species. In many of these as Bosmina obtusirostris, Daphnia hyalina (other than the variety lacustris), and Diaphanosoma brachyurum, the gut-contents normally consist of particles so very finely divided as to be unidentifiable. In Daphnia longispina, Daphnia hyalina lacustris, and Ceriodaphnia pulchella the principal gut contents are very small algae and particles of detritus, whilst in the pond Daphnias and to a lesser extent Bosmina longirostris, quite large particles may beconsumed. It is of interest that this graduation corresponds fairly well with the size of the water-bodies that the species normally occupy. It seems probable that the impossibility of identifying algal remains in the guts of the Cladocera from larger lakes, is a result of the extreme delicacy of the Algae on which they feed. Other evidence (see below) suggests strongly that they are algal feeders. Of the other species all save two show a preponderance of algal feeding over detritus feeding when only flourishing populations are considered, these are

Ceriodaphnia pulchella and *Daphnia longispina* which both appear to consume considerable quantities of detritus though also taking much algal food. However as the records show, populations may be found in which the individuals have fed mainly on detritus. In all such cases I have found that on examination of the water by iodine precipitation there was only a very scanty population of Algae, and in all these cases the Cladoceran population was obviously not flourishing.

The size of particles consumed by large lake forms is consonant with the filter feeding hypothesis, but the other species, and especially the pond Daphnias and *Bosmina longirostris* often consume particles of very large size. With these species as with the bottom-living forms the largest particles consumed correspond very closely in width with the diameter of the mid-gut. It is also evident that the factors governing digestibility of Algae in these species are similar to those operating in bottom living Cladocera. It is interesting that, contrary to the views of Pacaud, many ohecate flagellates, as *Trachelomonas ~~votrecina~~ volvocina*, are readily digested by pond Daphnias.

I cannot however detect any good evidence for selective feeding. The gut-contents usually approximate closely to the particles of similar size in the surrounding medium. Admittedly certain large species may not be consumed even though they are abundant, and I have actually observed individuals of *Daphnia hyalina* s.s. repeatedly rejecting colonies of Coelosphaerium. Nevertheless my general impression is that these planktonic Cladocera are to a great extent indescriminate feeders. It may well be, however, that they congregate in regions where there is an abundance of small algae, but such an investigation was outside the scope of my survey.

The question arises as to whether the observed distribution of species of Cladocera corresponds at all well with their food-requirements as deduced from their gut-contents.

It must be born in mind for this purpose that a record of many individuals from a locality is of more weight than a record of one individual, and similarly individuals with many eggs areof more weight than individuals with few eggs.

Unfortunately it was not possible to devise a method of quantitive collection which was both exact, and applicable to all the different types of habitats I studied. On the other hand it was desirable to obtain collections from as many different types of habitat as possible for the reasons given in part 2 (see above). I had therefore to content myself with making collections as nearly comparable as possible and estimating the abundance of the different species.

Egg-number can of course be accurately determined, but the highest egg-numbers likely to be attained vary from species to species. Thus the actual egg-number would be misleading as an estimate of the flourishing nature of the colony. I found it advisable to record the egg-numbers as high, medium, or low, counting animals with no eggs as having a very low egg-number.

It is not possible to obtain exact quantitative figures for bottom algae and detritus so that the results for these had again to be expressed in terms of relative abundance. Only particles small enough to be eaten by the species were considered in these estimates.

The observations which I have made suffer thus from an inevitable vagueness but they do form a suggestive qualitative picture, which agrees very well with the conclusions I have reached from an examination of gut-contents. The observations I have made are too numerous to include here, but table 16 based on results that I obtained at Wray in the summer of 1949 can be taken as typical.

In this table I have adopted a short-hand formula to include the frequency, abundance, and relative egg-numbers of the various species. The various items in this formula are explained in the footnote to the table. Nine grades of abundance were recognized ranging from extremely abundant, where several hundred individuals could be obtained by a single short sweep of the collecting net, to extremely scarce where only one or two individuals were obtained after prolonged collecting. These grades were awarded the numerical values 1 to 9. Egg-number was estimated as very high, high, medium, low, and very low, and these were given the numerical valuesl to 5. In the case of the Chydorines those populations in which most individuals had two eggs were given the value of 5, those in which the numbers of empty individuals, or individuals with 1 egg equalled or exceeded the number of individuals with two eggs were given the value 3, whilst those in which the vast majority of individuals were empty were given the value 1. I do not claim any theoretical significance for this formula, which I have adopted solely on the grounds that it condenses unwieldy observations into a manageable form whilst still showing their main features. It is clear that any useful formula must include the frequency, abundance, and egg-number of the species, as this formula does, but the only justification I can give for multiplying the three items of information together instead of adding them is that by this means I obtained figures that better expressed the conclusions that I had drawn from my observations, than I did by adding them.

The table shows that the distributions of the species are strongly in agreement with their principal food as determined by an examination of gut contents. At the time I had not determined the gut-contents of ~~*Peracantha*~~ Pleuroxus *truncat*~~*a*~~us and *Alonopsis elongata*, but these field observations enabled me to predict, what I afterwards found to be true that ~~*Peracantha*~~ Pleuroxus *truncat*~~*a*~~us feeds largely on Algae, whilst *Alonopsis elongata* is mainly a detritus feeder. Thus observations of the distribution of littoral Cladocera confirm the conclusions dervied from the study of their gut-contents, that they fall into two groups of algal and detritus feeders.

Since that date I have collected many more records of these and other species, but as they merely confirm the conclusions I have reached, I shall not deal with them in detail. Two cases of change in relative abundance of species, which I have observed, seem to be connected directly with changes in the nature of the available food. During August 1949 there was an abundance of bottom algae in Low Wray Bay, Windermere, and this was correlated with an abundance of *Sida crystallina*, and *Simocephalus vetulus*. Later, at the beginning of September the algae had become much scarcer, but detritus was more abundant. Collections showed that *Sida crystallina* was scarcer, but *Eurycercus lamellatus* more abundant, whilst *Simocephalus exspinosus* had been largely replaced by *Simocephalus vetulus*.

The investigation of the distribution of planktonic Cladocera, and the pond Daphnias, in relation to algae, proved to be much more difficult. In such an investigation it is useless to consider only the algae caught by a phytoplankton net since most of these are too large to be regularly eaten by Cladocera. They also form only a very small fraction of the algae produced in most lakes. It is necessary to examine the total seston (I.E. the total suspended matter on the water). There are various techniques for obtaining samples of the total seston. The most convenient, which I adopted is to collect a known volume of water, and precipitate its contained matter by means of iodine. The seston can thus be concentrated and its total volume obtained. Since we have not a reversed microscope in this laboratory it was necessary to adopt an improvised method of making algal counts. A drop of concentrated fluid was placed on a microscope slide and the numbers of the various types of algae, detritus, ciliates and bacteria in 20 smaple fieldas were counted. The observations were made with a x40 objective. Owing to lack of apparatus it was only possible to obtain samples from the surface layers of the pools and lakes examined, so that the results were not fully representative of the conditions throughout the habitat.

Collections of Cladocera were also confined to the surface layers. Since it was clearly impossible to obtain exact quantitative collections for all habitata, the results of these collections were expressed in general terms of relative abundance.

I have made such joint observations of algae and Cladocera at frequent intervals on the Lake and pools in Regent's Park, and have also made occasional, less thorough, observations on other habitats, during a period of just over a year. A large and somewhat chaotic mass of data has resulted which I have not yet succeeded in reducing to simple formulation. For this reason I shall not give these results in detail here, since the full original data would not be informative, whilst any condensations that I may make at this time would be misleading. However, whilst for the most part, my results do not indicate any definite conclusions, and so fall into line with the experience of the majority of investigators, a few special features are worth noting. A point of particular interest that has emerged is the association of Daphnia cucullata with lakes and pools in which small Chrysophyceae and other flagellates or the smaller Cyclotella spp. are abundant. In appendix 2 I have given all the records I have for this species, in which I also have records of the algae present. It is obvious that it is more strongly associated with these small organisms, than with the Myxophyceae. In the past the species has been considered to be especially characteristic of those eutrophic lakes which have rich populations of Myxophyceae (Wesenberg-Lund 1926, Wagler 1923). This apparent correlation with eutrophic lakes seems to me to be largely accidental. As is well-known (Wesenberg-Lund 1926, Wagler 1923, Berg 1931) Daphnia cucullata is more characteristic of shallow lakes than is D.hyalina; this tendency to occur in shallow lakes, coupled with its apparent need for a very rich nannoplankton, will normally result in it occuring mainly in eutrophic lakes. Under special conditions however it might occur in habitats that were not particularly eutrophic, provided that suitable food Algae were abundant. The localities which I list from Jutland are all considered to be comparatively oligotrophic, by the staff of the Hillerød laboratory, whilst Hampstead 3 does not appear to me to be very eutrophic.

A less definite, but still well-marked correlation between the flourishing nature of the Daphnia populations and the available small Algae is shown by the Daphnia spp. in the pools in Bedford College Botany Garden. Records for one of these pools are given in appendix 3. The behaviour of the populations in this pool can be taken as typical of all of them.

It is clear therefore that the occurence and abundance of some planktonic Cladocera is associated with the presence of an adequate food-supply in the form of nannoplankton Algae. This may be true for the other species also, but my records for them are subject to too many complicating factors for me to state this with certainty.

An observation which is of interest in view of the small size of the particles consumed by Cladocera in larger waters is the relative abundance of the more minute species of algae in lakes as compared with typical Daphnia ponds. This is clearly brought out in table 17 where I have given the percentages of algae which normally attain a size of less than 20 μ in different collections from Regent's Park Lake and some Daphnia ponds. Thus the generally smaller size of the algae consumed by planktonic Cladocera from larger waters as compared with those consumed by pond Cladocera, may be partly a reflection of a smaller average size of the available algae, in the habitat.

My algal records are of some interest from a purely algological viewpoint, quite apart from their connection with Cladocera. Nannoplanktonic algae, and especially those of pools have not received much attention in the British Isles. Thus many of the species which I have found appear to be rare, on the basis of published records, and several were not discovered until after the publication of West and Fritsch (1926). Certain of them seem, nevertheless to be somewhat common in the pools and small lakes around London. Particularly common is Spermatozopsis which I have found in most of the habitats which I have examined. Other supposedly rare species which I have found not uncommonly, include Nephrochloris angulata, Chodatella subsalsa, and Chroomonas acuta. 'Rarities' which I have found less commonly are Scourfieldia cordata, Elakatothrix gelatinosa f. biplex, Stenocalyx monilifera (recorded by Lund 1942), Pseudokephyrion conicum, a beautiful and distinctive species not previously recorded, spp. of Kephyrion and Kephyriopsis, Pyramimonas and Brachiomonas westiana. The last two species have been known from Regent's Park Lake for some years, and still occur there. A common diatom in this lake, which I had recorded as Cyclotella species, was identified for me by Dr. Lund as Stephanodiscus dubius not previously recorded from Great Britain. The lake has also a somewhat peculiar Cladoceran fauna, but unfortunately insufficient is known concerning the detailed distribution of the smaller Algae in the British Isles, for one to be able to draw any safe conclusions from this coincidence.

Culture observations.

My experience with the culturing of certain Cladocera has a bearing on the question of their normal food. As I have pointed out above I have never obtained really flourishing cultures of pond Daphnias, when I have fed these on bacterial infusions. This suggests that these species are not primarily bacterial feeders. On the other hand flourishing cultures are obtained with Chlorella, which is in agreement with my conclusions from other observations that these species are primarily algal feeders. Other species which I have reared successfully on a diet of Chlorella include Daphnia hyalina lacustris, Ceriodaphnia dubia, Moina macrocopa, Moina rectirostris, Bosmina longirostris, and Macrothrix hirsuticornis. On the other hand I have not been very successful in culturing Daphnia ambigua and Daphnia cucullata by this method. The adults appear to flourish and lay eggs but very few of the young survive. Chlorella is not an exceptionally digestible alga, and it may well be that the young of these species cannot digest it. My general experience with these cultures is that algae form a much more satisfactory food for many Cladocera than do Bacteria.

Yeast however seems to be jst as good a food As *Chlorella*, though it has other disadvantages as a source of nourishment in cultures. Thus it is probable that a number of small unicellular fungi, and perhaps also colourless flagellates are sometimes important sources of food for *Daphnia*. However such forms are normally very much rarer in nature than the nannoplanktonic Algae and so are not normally of great importance in the ecology of species of Cladocera.

Method of feeding.

Whilst I have not been primarily concerned with feeding methods, some of my observations do have a bearing on them.

I have noted that the majority of workers have assumed that the Cladocera are filter-feeders, though on inadequate grounds. If this were the case one would expect that the closeness of the filtratory setae would be correlated with the size of the food-particles consumed. Moreover it would not be likely that the size of the food-particles taken would be much larger than the size of the meshes of the 'filter.'

In order to test whether this was so in various *Daphnia* spp. I decided to examine closely the setae on the 'filtratory' endites. It was necessary in addition to examine the spacing of the setules on these setae as they also limit the pore-size of the 'filtratory' grid.

This proved to be a diffi~~l~~cult and lengthy task so that only a few individuals could be examined. Since it was necessary to examine the limbs under very high powers, they had first to be dissected out and permanently mounted. Euparol was chosen as the permanent mountant, since it is easy to use and has a lower refractive index than Canada Balsam, thus making the finer chitinous structures easier to observe. I also found it advantageous to stain the limbs with a chitin stain. Three such stains were tried, Light Green C.T. no.670, Chlorazol Black (as described by Cannon 1937, 1941), and Lignin Pink (also described by Cannon 1941). The last proved to be the most satisfactory when used in conjunction with a green filter. The animals were stained prior to dissection. This had two advantages, there was less chance of losing the dissected limbs, and the staining could be allowed to proceed for an indefinite length of time, according to convenience.

For dissection the specimen~~s~~ was placed in a drop of a 50% mixture of Euparol and Benzyl Alcohol, which remains fluid indefinitely, and the dissection was performed by means of a Harding micro-dissector (Harding 1939), using tungsten needles. The dissected limbs were then transferred with a fine mounted needle to drops of the Euparol-benzyl alcohol mixture on another slide. When a whole series had been obtained this mixture was sucked off, using a very fine semi-micro-pipette, and replaced by drops of Euparol, the whole was then covered by long cover slip. After standing in a warm room overnight the slides were dry enough for examination.

The slides were examined using a Cooke Troughton research microscope with a monocular eye-piece of x 12 magnification, containing a $\frac{1}{4}$ mm. eye-piece grid. Ordinary illumination was satisfactory for counting the setae but special methods were necessary for counting the setules. For this purpose a 1/12 inch or a 1/16 inch oil-immersion objective was necessary. An achromatic oil-immersion condenser was used. I found it best to use an ordinary achromatic microscope lamp, with the beam so arranged that it did not focus exactly in the centre of the microscope field but slightly to one side, the condenser also being slightly out of focus. I cannot justify this by theoretical arguments but it certainly gave better definition than normal methods of illumination. Setae and setules were counted by means of their basal insertions

The results which I have obtained are given in table 18. It soon became obvious that too many possible causes of variation were involved to enable me to use them to check the 'filtration' hypothesis in detail. Thus the closeness of both setae and setules varies with the age of the individual, the setae being much closer together in young individuals. I have not been able to detect any striking differences in the food of young and old individuals, but it is possible that the associated size difference ofsets the effect of the difference in closeness of setae. In favour of the filtratory hypothesis is the fact that the setae and setules are more closely set in the more lacustrine species. Here again however there are associated differences in size, which might in this case be the real cause of this apparent correlation between the lacustrine habitat and the closeness of the setae.

Several features do not favour the filtratory hypothesis. Thus the closeness of the filtratory setae does not exactly parallel the closeness of the setules. The closeness of the setae and the setules shows rather wide individual variation and may be different on different limbs of the same animal. Finally, even in *Daphnia magna*, the setules are extremely close together. The distances between setules of about $\frac{1}{2}\mu$ to 2μ are very much less than the average size of the particles which I have observed in the guts of these species. No doubt some filtration inevitably occurs, and these figures show that it would allow *Daphnia* to obtain particles of colloidal dimensions. This agrees with the conclusions of Gellis and Clarke who showed that *Daphnia* can utilise colloidal organic matter to a limited degree. However since these very small particles are a very subsidiary source of food, it is not easy to see why the 'filtratory' setae are so closely set.

Thus the results do not enable me to give a clear verdict on whether or no *Daphnia* is a filter feeder, though they make it clear that filtration of very small particles is possible. My observations have convinced me, however, that filter-feeding is not in itself adequate to explain the type of food taken by many Cladocera. I find it impossible to assume that very large Algae such as *Botryococcus*, or filamentous Algae such as *Tribonema* are filtered off by the thoracic limbs. Many of these forms are, in fact, considerably longer than the interspace between the filtratory limbs.

I have noted that Lochhead (1936), whilst adhering to the filtratory hypothesis, remarks that in *Penilia avirostris* the majority of food-particles which he observed passed straight into the ventral food-groove, without approaching the 'filter' setae. I have on several occasions watched *Sida crystallina* and *Simocephalus vetulus* feeding, and can confirm that in both these species the food-particles mostly pass directly in the ventral food-grove, without approaching the lateral setae. I have not been able to check this for *Daphnia* since it is not possible to obtain such a clear ventral view of members of this genus. Thus in several species of Sididae and Daphniidae the filtratory hypothesis cannot possibly hold, and further evidence will be necessary, before it can be considered to be established for any.

On the evidence at present available it is,more correct to term these forms vortex feeders.

If the primary function of the 'filter' seatae is not filtration, some other explanation is necessary for their marked regularity. My own idea is that they function in a manner intermediate between that of valves and that of aerilons, at once controlling the strength of the feeding current and its smoothness. If this were so it would perhaps agree with the observation that they tend to be more closely set in the larger species, since more open setation would presumably allow a more powerful current to be produced for the same expenditure of energy. The open-ness of the setation would however be limited by ~~turbidity~~ turbulence effects. Unfortunately I am not sufficiently aquainted with the principles of hydrodynamics to judge whether or no this theory is mechanically feasible and I have not been able to find anyone who could tell me this. Thus I merely hazard the idea as a possible explanation.

I am of the opinion that it is even less correct to describe many of the Chydoridae as filter-feeders, than it is for the Daphniidae. Even on morphological grounds alone it seems unlikely that such a mechanism could be of prime importance, since the filtratory endites are often of extremely small size in comparison to the other limb elements (see for instance the drawings in Lilljeborg's Cladocera Sueciae (1900)). On the other hand the first limb may be very large and somewhat projecting. Chydorus sphaericus, in particular, often appears to be scraping particles from the surface of filamentous Algae by means of these limbs, and such a feeding mechanism may be more general. Unfortunately I have not been able to interpret the exact feeding mechanism, owing to the small size of the individuals and the crowded arrangement of their limbs. It is, however, noteworthy that the gut-contents of some species, and especially

Eurycercus lamellatus suggest that they may feed by non-filtratory mechanisms. My conclusion from these observations is, that the feeding of Cladocera needs thoroughly re-examining; and that this re-examination should not be purely morphological.

Summary and discussion.

My conclusions with regard to the feeding of Cladocera may be summarized as follows :-

Littoral and bottom-living Cladocera can be divided into two groups; those which feed mainly on Algae, and those which feed mainly on detritus of vegetable origin. The occurence of these species corresponds very well with their food-requirements.

Some species certainly show selective feeding, but this may depend on selection of feeding sites,

With the exception of these species there seems to be little selection of particles, other than that between Algae and detritus, save that no particles are consumed greater than a maximum size, which seems to be determined purely mechanically by the internal diameter of the gut.

It is more difficult to define the food requirements of the more or less planktonic Cladocera, but several lines of evidence indicate that this is probably in most cases provided mainly by nannoplankton Algae. I have no evidence for extensive bacterial feeding in any species.

Planktonic Cladocera, seem to be largely unselective in their method of feeding, and several species can exist, though not flourish in the absence of Algae. Daphnia longispina is probably less dependent on Algae than most species; but Daphnia cucullata on the other hand appears to be absolutely dependent on the presence of adequate supplies of minute Algae.

Feeding observations, and the examination of gut-contents suggest that true filter-feeding is not the most important method of feeding in many species. The Daphniidae and Sididae are perhaps best described as vortex feeders.

The digestive powers of different species of Cladocera vary considerably, nevertheless certain general statements can be made in regard to the digestibility of Algae. As Lefèvre stated, small thin-walled Algae seem to be more digestible than large thick-walled species. However this statement does not apply to forms with pores in their cell-walls, which are often readily digestible; or to forms which are enveloped in large masses of mucilage, which are often indigestible.

Part 2. General ecological survey.

In addition to the rather thorough investigations of food and temperature which I have dealt with above, I have made a general survey of the ecology of the Cladocera, based on field-collections in a large number of localities in England, Scotland, and Denmark. In some areas as in S. Yorkshire, and the London area, I have been able to make collections in all seasons, but in Scotland, the Lake District, and Denmark, my collections were confined to the summer months.

In all habitats I used standard collecting methods; but for investigating the distribution of littoral Cladocera I used a small net only $5\frac{1}{2}$ inches in diameter, instead of the more usual 8" to 10" net since this enables me to localise the origin of my collections more exactly.

The ~~eco-distribution~~ Ecological distribution of non-planktonic Cladocera has been little studied, and the group has usually been neglected by general ecologists, so that there are comparatively few surveys with which mine can be compared.

The most important of these for western european forms are those of Poulsen (1928), Berg (1929, 1931), and Pacaud (1939). A number of surveys of limited areas in the British Isles such as those of Scourfield on the Entomostraca of Epping Forest (1898), and of N. Wales (1895); of Gurney on the zooplankton of the Lake district (1923), which also includes reference to the non-plankton species of the high tarns; and of Jenkin (1928) on the Cladocera of Wicken Fen, are also of interest. A number of other papers are of more limited interest, and I shall refer to these when they have some bearing on my results.

Following the pattern introduced by Danish authors I shall give first a survey of my records and conclusions concerning individual species, and follow this by discussions of the more important environmental factors in relation to the whole group.

<u>Sida crystallina.</u>

Loch Altabruig, 31.8.48., very scarce; Loch a' Phuirt Ruaith, 7.9.48., very numerous; W. Loch Eilean a' Ghille, 8.9.48., abundant in weeds; Loch Teanga, 9.9.48., abundant, males present; Loch Druidibeg III, 9.9.48., Scarce; hill pool, Loch Skiport, 9.9.48., one male only; Wray Boat Dock, Windermere, 5.8.49., very abundant, 12.8.49., very abundant, 30.8.49., numerous eggs low; Wray Boathouse, Windermere, 12.8.49., not numerous, eggs high, 30.8.49., numerous, eggs low; Wray Jetty, Windermere, 8.8.49., very abundant, eggs high, 12.8.49., extremely abundant, eggs high; 30.8.49. numerous eggs low; Low Wray Bay, Windermere, 5.8.49., scarce, 8.8.49., very abundant, 12.8.49., scarce; Borran's Field, Windermere, 6.8.49., behind reeds, scarce, eggs moderate; 11.8.49., not very numerous, eggs high; Pull Wyke, Windermere, 12.8.49., outside reeds, very scarce; High Wray I, Windermere, 16.8.49., not numerous, eggs low; High Wray II, Windermere, 16.8.49., numerous eggs low; Blelham Ic, 4.8.49., numerous; Blelham Ia 18.8.49., not very numerous, eggs high; Blelham II, 8.8.49., scarce, mostly young; Blelham IIIa, scarce; Blelham IIIb, 1918.49., very abundant eggs high; Blelham Iva, 19.8.49., not very numerous, young only; Blelham Outflow, 8.8.49., very abundant; Tarn Hows I, 13.8.49., very scarce, young only; Tarn Hows II, 13.8.49. not numerous, mostly young, 27.8.49., very scarce young only; Tarn Hows III, 13.8.49., very numerous, eggs low, 27.8.49., very numerous; Coniston I, 13.8.49., very scarce; Coniston III 20.8.49., numerous, eggs low to moderate; Wharton Tarn, 14.8.49., abundant eggs moderate; Wray Mires II very numerous, eggs high; Wiseen II, abundant, eggs low; Elterwater, 30.8.49., young only; Hampstead 1, 1.11.48., not very numerous, males present; Hampstead 2, 1.11.48., scarce, males present; Hampstead 3, outside reeds only, scarce, males present; Little Stanmore 2, 9.7.49., numerous in Potamogeton, scarce in clear water, 12.10.49., not very numerous in thin and scarce in thick weeds, eggs low; Highgate 2, 5.7.50., very numerous in clear, abundant in thin flags, eggs moderate; Highgate 3, 5.7.50. not very numerous, mostly young, eggs moderate; Badstue Dam, 20.7.50., very scarce, eggs high; numerous, most young, adults 16, and 7 eggs; Frederiksborg Slotssö I, 21.7.50., not numerous, young only; Slotssö II,21.7.50., one young; Slotssö, III, 25.7.50, numerous, young very numerous, eggs very low; Slotssö IV, 9.8.50, numerous, eggs low; Teylgaard Sö, 22.7.50., numerous, eggs low, at edge of reeds, very numerous, all young, in Nuphar; 2.9.50., not numerous, young only, thick reeds, scarce, young only in clear water;

Esrum Sö I, 25.7.50., very numerous, eggs low; Bastrup Sö, 10.8.50., young numerous, adults scarce, eggs low, in moderate reeds; Karlssö, 19.8.50., very scarce, mostly small; Arressö II, 22.8.50., one with few eggs; Arressö III, 22.8.50., very numerous, eggs very low; Madum Sö II, 9.8.50., numerous, most young; Madum Sö, III, 9.9.50., abundant; Madum Sö IV, one young only; Borressö, 10.9.50., very numerous in *Nuphar*, numerous at edge of reeds; Almindsö, 11.9.50., very scarce, young only.

Except for details most authors are agreed on the principal features of the ecology of this species. It is known as a form characteristic of the weedy margins of larger waters, or more rarely pools with clean water. According to Poulsen (1928), and Pacaud (1939), it is most usual in moderately acid to moderately alkaline waters.

Brown (1929) considers that it is a cold-water species, but Poulsen (1939) states that its northern limits are Iceland and Scandinavia, and that it is commoner in Central than in Northern Europe.

My results agree well with this general opinion. The restriction to weedy waters is not absolute as the records from the Hampstead and Highgate Pools show. The species appears to avoid very thick vegetation, and as Berg (1929) states, it is much commoner amongst *Nuphar*, *Potamogeton*, and similar plants, than it is in reed-beds. Strangely Poulsen (1928), seems to hold the opposite opinion. It is probable that these preferences are a reflection of its algal diet (see above.)

My results indicate that in western Europe it is neither a cold-water nor a warm-water form. I have rarely found it in winter, which suggests that in England, as in Denmark (Berg, 1929), it does not normally survive the winter as adult individuals.

Diaphanosoma brachyurum

I have records of this species from the following habitats: Windermere, inshore after a storm and very scare; Blelham, several stations, and numerous at some; Codale Tarn, very scarce; Wray Mires I, scarce; Wiseen II, very scarce; Derwentwater, very scarce; Rydalwater, abundant, few eggs; Badstue Dam, 20.7.50., scarce eggs low, 30.8.50., very numerous, eggs low; Teylegaard Sö, 22.7.50., not numerous, males, 2.9.50., very scarce, males and ephippial females; +Log Sö, very scarce, eggs 0 ; Ö Dam, scarce, eggs very low; Bure Sö, plankton only eggs low; Arressö, I, scarce, young only, II, very numerous, males, III, very numerous mostly young, IV, one young only; Ellessö, collection was in thick reeds, one without eggs.

In my records for this species I have treated D. leuchtenbergianum, as a mere form, following Berg (1929) and Rylov (1935). Individual variation is considerable, and I have found more than one population showing all intermediates between the two supposed European species. For similar reasons I have not attempted to distinguish the various described varieties, indeed the majority of the populations which I have examined could not be ascribed to any described variety. The whole genus is in need of thorough revision (see for instance Brehm 1933), and until this has been performed no useful purpose can be served by attempting too fine descrimination in such a study as this.

The genus as a whole is most abundant in the tropics, and D. brachyurum is also to some extent southerly in distribution, reaching its northern limits in the British Isles and Scandinavia. It is also a summer species (Wesenberg-Lund 1926). My records suggest that it may have already past its apogee by late July, as none of the populations which I have found were really flourishing. On the other hand it seems unlikely that temperature is the principal restricting factor in the northern portion of its range. I have found it in Codale Tarn at an altitude of 1528 feet, whilst Gurney (1923), records it as the dominant crustacean in October, in Greendale Tarn, altitude 1320 feet, when the water was 'very cold.' The species is a typical planktonic form, though sometimes found in ponds, and amongst weeds, (Poulsen 1928, Berg 1929), and my records agree with this.

Except for the record from Codale Tarn all my records are from alkaline or slightly acid waters; but I attach no importance to this, as several investigators have found it in strongly acid waters (Harnisch 1929), Hubault 1932, Krasnodebski 1937), Pacaud (1939) only finds it in strongly acid localities when these are peaty; whilst Poulsen (1928) states that it is rare in strongly acid waters.

Though I have found the species in pools, I have not found it in very small pools. A point of interest is that I find it much easier to collect this species in the littoral region of smaller waters than in the littoral region of larger waters. In this it agrees with a number of planktonic forms. The observation has a bearing on the question of 'littoral' avoidance.' A somewhat surprising feature is the apparent rarity of this species in the London area, where there are a large number of apparently suitable habitats. It is recorded from the area (Baird 1850, Scourfield 1898) but I have not found it, and it has never to my knowledge occured in any of the numerous collections made by our limnology students in the past three years. It is difficult to suggest a reason for this, though it may possibly be a consequence of atmospheric pollution.

Latona setifera.

Tarn Hows I, 13.8.50., scarce, 27.8.50., scarce; Tarn Hows II 27.8.50., very scarce, high egg number; Coniston II, 13.8.50., very scarce; Badstue Dam 20.7.50., scarce, mostly young; Storre Gribsö II, 3.8.50., scarce, egg-number very low; Storre Gribsö IV, 3.8.50., very scarce, egg-number very low.

The recorded opinions on the occurence of this species are so conflicting that it is impossible to reconcile them. Birge (1918) states that it is widely distributed, though scarce amongst weeds in ponds and lakes, in N. America. Berg (1929) says it is found in Denmark only in miry places at $\frac{1}{4}$ to 2 ms depth in small lakes and ponds. P.E. Müller (1858), holds similar views, whilst Lilljeborg (1900) gives a similar distribution in Sweden. Scourfield (1912) records it from a small peaty pool in western Ireland.

Opposed to these views, Scourfield and Harding (1941) say it occurs on the bottom near the shore, and to moderate depths in lakes; whilst G.O. Sars (1865) says that it occurs only in fairly large lakes, and never near the shore, being commonest at about 2 fathom. Pacaud (1939) does not record it from ponds in France.

Scourfield's list of Lake District Cladocera (Scourfield Ms.), shows that the species occurs in a number of the large English Lakes.

It seems clear from this that there must be biological differences between the ~~super-populations of~~ representatives of this species in different parts of ~~the species~~ its range. My collections support this hypothesis. My two English records are both from large waters. In both, the bottom was stony, rather than muddy, and the individuals were obtained from exposed shores at depths of ½ to 2 metres. Since according to Berg (1929) *Latona* is a well-adapted burrowing form (though in my opinion it rather rests on the surface of mud than sinks into it), it seems probable that the specimens I caught were strays from deeper water. Despite the large number of lakelets and small ponds in which I have collected, I have not found it elsewhere in England. On the other hand I succeeded in rediscovering it in both of Berg's Danish Localities, in which I collected, in places where the bottom was largely of sand and silt, though perhaps not strictly miry. It did not appear in any of my collections from larger Danish Lakes, even from stations which would appear to provide suitable habitats.

The possibility that there are really two very similar species confused under the one name, must be borne in mind. However, though I have seen too few specimens to examine this critically, I think that it is unlikely. There are certainly no obvious differences between the Danish and English forms. Thus it would appear that there are, rather, a number of races, separated both geographically and ecologically, but showing little or no morphological difference.

Holopedium gibberum.

Windermere, North Basin, 8.3.48., one only; Grasmere 30.8.49., scarce, large; Rydal Water 30.8.49., very numerous, all small.

My few records do not allow me to add much to what is already known concerning this strange species, the ecology of which has been rather thoroughly treated by Thienemann (1926), and

The species is common in Grasmere and Rydal Water throughout the summer (Scourfield Ms.), but it seems more usually to disappear after late spring. This probably accounts for my failure to find it in S. Uist, where it almost certainly occurs. It was certainly absent from Madum Sö at the time of my visit, though this lake is famous as its only known Danish locality.

The genus Daphnia.

I have treated the systematics of this genus at some length in a paper, now ready for the press. I am including a manuscript copy of this paper with my thesis.

It is rather difficult to obtain accurate records of the natural occurence of the pond Daphnias, since in a number of ponds in which they occur, they have certainly been introduced, whilst in others they probably have been. Thus the figures for the relative abundance of these species derived from habitat counts in an area such as the London area may be grossly misleading. In the following I have ignored all records for localities in which there is a suspicion of deliberate introduction, except for the pools in Bedford College Botany Gardens. At one time or another in the few years prior to the commencement of my research, representatives of almost every pond species save Daphnia atkinsoni, had been introduced into almost all the pools. In particular I know that D. magna was introduced into the Water Lily Pond, and Pool 2, of the main series, but failed to survive. When I first commenced to investigate these pools no introductions had been made for some time, and the species present had become sorted out into populations which have remained fairly characteristic of the different pools ever since. Thus these pools provide an opportunity for studying the selective effect of environment, without the usually complicating possibility of accidental absence or presence.

Daphnia magna

Ringmere, Thetford, 10.7.48., one ephippium; Trough I, Hampton Water Works, 25.11.48., numerous, egg-number high; Trough II, Hampton Water Works, 25.11.48., very scarce, mostly young; Thames at Hampton 27.1.49., a few ephippia; Brent Decoy Pond, 27.11.48., abundant, 6.1.49., abundant some ephppiate; 29.4.49., a few large old individuals,many young, 12.5.49., very numerous, in swarms, few eggs, few are large; 23.5.49., very numerous, few large, egg-number low, 3.6.49., very numerous, very few old, 7.6.49., abundant, in swarms, egg-number low, some ephippiate; Pool 5, Botany Garden 21.10.49., numerous, eggs c.12; 8.11.49., numerous, eggs 4 (1 to 8), 22.11.49., numerous, no eggs, 12.12.49., under ice, scarce, no eggs, 16.1.49., 8°C, scarce, no eggs, 25.4.50., numerous eggs c.20, some males, 7.6.50., 21°C very numerous, 10.7.50., 17.5°C, abundant, egg-number 15.1 (10 to 22); 8.8.50, abundant, eggs c.10 (8 to 12), 14.10.50., abundant, egg-number 4.6 (0 to 10), 17.11.50., almost all empty; Pool 4, Botany Garden, 21.10.49., very abundant, eggs 6 to 12, 8.11.49., numerous, eggs 0 to 8, 12.12.49., under ice, one male; Pool 4b, Botany Garden, 22.11.49., scarce 0 eggs; Pool 7, Botany Garden, 8.11.49., scarce, 22.11.49., scarce, 0 eggs, 12.12.49., under ice, very scarce, no eggs, 7.6.50., 23°C, scarce, eggs 4, 8.8.50., very numerous, mostly young, 14.10.50., numerous all apparently empty, 17.11.50., abundant, all empty.

There is very considerable difference of opinion on most points concerning the distribution of this species, which one can only conclude must affect somewhat different habitats in different countries.

Scandinavian authors, as Berg (1931), and Wesenberg-Lund (1926), consider that it is almost completely confined to small, highly polluted village ponds. Pacaud (1939) has never found it in such pools, and on the basis of his own experience and that of Grasse (unpublished), he concludes that the species is characteristic of small pools with much suspended matter but not very highly polluted.

Scourfield and Harding (1941), regard it as rather rare, occuring in warm waters, in small ponds, or little bays of larger waters. It has a southern distribution in this country. On the other hand Brown (1929) disagrees with most European author's, in considering it a northern, cold-water form.

In regard to habitat, my experience agrees with that of Pacaud, rather than that of the Danish authors. The species is recorded from highly polluted, cattle ponds, in this country, but I have never found it in such places, except in the ground s of the Zoological Society, where it has certainly been repeatedly introduced. Of the many records of Daphnia localities, which we possess in this department, none of those for D. magna refer to this sort of habitat. With one exception, my localities, and those known to me, are slightly polluted, rather turbid pools, from $\frac{1}{2}$ to 2 ms deep. Most are small, but Brent Decoy Pond is of moderate size. On the whole the species seems to prefer slightly larger and deeper habitats than D. obtusa, with which it may often be associated. It is noteworthy that the only pond in the college Botany Garden, in which it has firmly established itself is the largest and deepest of the main series. The reocrds from King George VI Reservoir are of great interest. The specimens obtained from this locality were taken by a surface plankton tow in water of adepth of about 15 ms. The population appeared to be firmly established. Daphnia *magna* is considered to be *the* pond-Daphnia, see for instance Wesenberg-Lund (1926), and I know of no instance where it has been recorded from the plankton of a large body of water, though the probably derived *D. lumholtzi* is strictly planktonic, whilst the allied *D. carinata*, has given rise to a whole series of planktonic races (Wagler 1936), The only unusual feature that I could discover concerning this reservoir was that it had only been filled permanently for a few months. Prior to that ~~time~~ there had been for some time a few small pools in the bottom. It seems that *D. magna* may have been established in these pools which would serve to innoculate the reservoir. One would be tempted to ascribe its continued presence to absence of competition but it is rather difficult to see how it would compete with the much smaller lacustrine Daphnias; and, in any case, *D. longispina* is already established in the reservoir. At any rate it is at least clear, that in some circumstances *D. magna*, can survive under lacustrine conditions. This observation is important in lessening the apparently large gap between lake and pond Daphnias.

Berg considers that some populations survive the winter, but that no reproduction occurs when temperatures are consistently below 5°C. This agrees with my records, again with the exception of that from King George VI reservoir. The temperature at the time of the latter collection from here was 4.5°C, and Mr. Ryley informs me that the temperature had not varied much from 4°C, for several weeks previously. Yet, in each collection a proportion of the individuals had some eggs, and many young were present in the second collection. This seems to be another illustration of the rule that large size of habitat may compensate for adverse conditions (Macan 1950).

Daphnai atkinsoni

Tree Pool, Berrylands, 25.1.49., numerous, 26.3.49., very numerous, 6.4.49., not very numerous, eggs low, c. 60% ephppiate, 6.3.50., abundant, many ephippiate, 23.3.50., abundant, many males, many ephippiate, 30.3.50., abundant, almost all males and ephippial females, a few with c. 10 eggs; 18.1.51., not very numerous, eggs 6 to 12; x.12.50., scarce; Berrylands Ditch, 6.4.49., very scarce, males and an intersex present, 18.1.50., not very numerous, eggs 6 to 12; Witt's Farm, God's Hill, 31.10.49., abundant, egg-number c. 45 (40 to 70+), 8.6.50., not very numerous, eggs 2 (0 to 9), 24 C.

I have already discussed this species at some length and little need be added here. The habitats which I have seen do not give any clue as to the causes of the rarity of this species. They appear to share no obvious feature which is not also shared by most *D. obtusa* habitats, except a slightly greater maximum winter depth, which, however, is insignificant. The partial or complete replacement by *Daphnia obtusa*, which I have observed in both pools in hot waather, suggests that competition with this species may be one limiting factor. It cannot be a complete explanation, since, after all, the species has survivied in these two localities.

Daphnia pulex

Fowlmere, 10.7.48., one young, minnehaha form; Fowlmere Pool, 10.7.48., abundant, minnehaha form; Cripplegate, 14.11.48., abundant; Brent Decoy Pond, 27.11.48., abundant, 6.1.49., abundant, 29.4.49., numerous, many ephippia, 12.5.49., very scarce, 23.5.49., very scarce, 3.6.49., very scaree; Pool 7, Bedford College Botany Garden, 8.11.49., not very numerous, ephippiate, 22.11.49., abundant, eggs 0 to 4, mostly ephippiate, 12.12.49., numerous, 0 to 12, many ephippiate, under ice; Pool 8, Botany Garden, 21.10.49., not very numerous, almost all ephippiate, 8.11.49., not very numerous, mostly ephippiate, 22.11.49., numerous, 0 to 4 eggs, many ephippiate, 12.12.49., very numerous, egg-number c.6, many ephippiate, 16.1.50., very scarce, no eggs; Leg of Mutton pond, Hampstead Heath, 21.10.50., very abundant offshore, less so inshore, egg-number 1.5 (0 to 3), many had been ephippate, 14.10.50., offshore only, very abundant, many ephippiate, 9.11.50., abundant inshore and offshore, egg-number 3.8 (1 to 6), 20.1.50., none; Spejl Dam, 20.7.50., abundant, eggs 3 to 6; Lynge Dam 11.8.50., very numerous, egg-number 10.5 (9 to 14); Pipervang Pool, 25.7.50., one young only, many ephippia; Badstue Dam, 30.8.50., very scarce, margins only, eggs c.7.

Published information about this species is largely unreliable, except where it is applicable to the whole '*pulex*' group, owing to confusion with other species.

There is considerable doubt as to many of the requirements of the species. Thus Ström (1926) claims that it does not occur when the pH. is less than 6.5, but Passowicz (1935) has found the species (s.lat.) down to pH. 5.1, and Pacaud (1939), also dealing with the broad species, says it can live in humic localities from pH. 4.9 to 10, though most commonly in nearly ~~natural~~ neutral waters. He also states that it is almost invariably present in cattle polluted ponds, where these are not dystrophic, but such records probably refer mainly to *D. obtusa* and *D. curvirostris*. Wesenberg)lund (1926), on the other hand, states that it is characteristic of small, clear, particularly forest pools, and also the littoral region of the smaller lakes; but it is clear from his account that he confuses the species with

D. longispina.

Both Wesenberg-Lund and Ostwald (1904), state that the species (s. lat.), cannot reproduce under ice. This agrees with the records of Poulsen (1940b), and with my records, so far as *D. pulex* s. s. is concerned. On the other hand it will reproduce at very low temperatures in the laboratory.

Scourfield (1942) considers that it is more typical of larger and less turbid pools than *D. obtusa.*

It appears to be the only species of the group which occurs in the arctic, judging from published figures and descriptions (Poulsen 1939, 1940, Ekman 1904 etc.). It was certainly the only pond Daphnia present in collections which I have examined from Bear Island.

My collections strongly confirm the view that this species prefers larger pools than ~~does~~ *D. obtusa.* My localities are mostly of moderate size, and from one to two meters deep. They are slightly but only very slightly polluted. I have never found the species in heavily polluted ponds. It may occur in very small pools such as pools 7 and 8 in the college Botany Garden, and the Pipervang pool, which are all mere puddles. It may be significant that all of these contained many dead leaves. It is clearly less well adapted to these than the other species of the group, since it has subsequently been replaced by these in the college pools.

The larger pools which this species inhabits are admittedly less turbid than those that are typical of *D. obtusa*, but I doubt whether this has any real connection with the absence of ventral setae in this species. The setae are also absent in *D. curvirostris*, which inhabits similar localities to *D. obtusa*; whilst they are present in species of *Ceriodaphnia*, which are not found in very turbid habitats.

Daphnia pulex, is commonly spoken of as the common water-flea, but it is clearly rather rare in England, in comparison with most species of the genus. Its occurence strongly suggests that it is an unsuccessful form, which is restricted in it s distribution by competition with D. obtusa, and D. longispina. In the narrow range of habitats intermediate between those most characteristic of these two species it is the dominant Cladoceran.

Daphnia obtusa

I have records of this species from the following habitats; Hoober Pool, 413.982, S. Yorks, 19.8.49., very abundant; Statue Rond, Queen Mary's Garden, it was numerous throughout the winter 1948 - 1949, and was abundant by April, 1949, eggs 5 to 7; subsequently gold fish were introduced into the pool and by the middle of June it had disappeared though the last survivors showed a high egg-number; it re-appeared as a few individuals with egg-number c.20 in April 1950, but did not become numerous, though a few individuals were stilla few present on 17.8.50. Deep pool and Pool 1, Berrylands, abundant and flourishing throughout the lasttwo winters, it persists until the pools dry up; on 21.6.40., temperature 26°C, it was still numerous with 12 to 20 eggs; the highest egg-number I have recorded for this locality was 42; Newt Pond, Putney Heath, on several occasions, at all seasons in small numbers, though sometimes with high egg-number; Curling Pond I, Putney Heath, 24.3.48. : Kingsmere, Putney Heath, June and November, in abundance: Island Pond, Queen Mary's Garden, 28.4.49., scarce, 17.5.50., very scarce; Pools in Bedford College Botany Garden; it has occured in all these pools; it is sporadic in pool 2 and 8; it is well established in pools 4 to 5, and flourished in pool 7 in the early part of 1950; it occurs throughout the year, but is scarce and with few eggs in winter; the highest temperature I recorded was 25°C, at which temperature it never showed a high egg-number; it was largely replaced by D. curvirostris in the Water Lily Pond, in the summer of 1950; Glyceria Pond, Leystonstone, 30.10.49., numerous, no eggs; Snaresbrook Road Pond, 30.10.49., abundant egg-number 3.2; Bomb crater, Bookham Common, 20.2.50.,: Epping Forest, Pool 3, 25.3.50, 15.5°C, abundant in clear water, c.4 eggs: Leg of Mutton Pond, Hampstead Heath, 14.10.50., inshore, very scarce, deformed: Golder's Hill 2, 9.11.50., very numerous, all empty; Witt's Farm, God's Hill, 31.10.49., very abundant, egg-number 20, 8.6.50., very abundant indeed, egg-number c.12, x.3.50., none ; Groby 2, Leicester, 6.1.49., scarce, young only; Groby 3, Leicester, 6.1.49., scarce, very large, eggs over 20.

This species has so often been confused with varieties of D. pulex, that almost all records are worthless. The common opinion that it occurs only in more or less acid waters (Pacaud, 1939, Wagler, 1930), and Tauson's statement that too much calcium is detrimental to it (1931), must be due to such confusions. Certainly the species does occur in acid localities (the Curling Pond; Golder's Hill 2), but it is much commoner in less acid waters, and is in fact by far the commonest species of Daphnia in small ponds even when these are highly alkaline.

Scourfield (1943) states that the typical form at least is usually found in smaller and more turbid pools than D. pulex. I find this to be true also of the much commoner propinqua form. All my localities, and all others known to me, in England are small pools, and most are very small and less than 1m deep. In the two largest pools from which I have records (the Newt Pond, and the Leg of Mutton Pond) it is largely littoral.

The records show that the species is remarkably eurythermic. It can flourish at temperatures of about 25°C; but, in England, at any rate, it commonly survives, and reproduces throughout the winter.

In Bedford College Botany Garden it often occurs with D. curvirostris but the two species do not seem to be serious competitors.

Daphnia curvirostris.

Aldwarke Wash, 24.9.47., very abundard, 2.8.48., 4.6.49., scarce, 11.9.49., very numerous, 10.10.49., very scarce, 28.9.50., numerous empty, and on other occasions in early summer and late spring; Aldwarke Marsh, 16.8.48., numerous in cut Typha, eggs c. 15; Roadside Pool, Aldwarke, 4.6.49., very abundant in open, eggs high, 2.8.49., abundant, 28.9.50., pool overgrown, very numerous; Canal pool, Aldwarke, 3.7.50., very abundant, some ephippiate, deformities, 28.9.50., numerous, eggs moderate, some males; Trough 1, Hampton Water Works, 25.11.48., very numerous, many eggs; Trough 2, Hampton Water Works, 25.11.48., scarce, adults only; Statue Pond, Queen Mary's Garden, 17.8.50., very scarce; Pool 2, Bedford College, Botany Garden, 17.11.50., very scarce, males and ephippial females; Botany Garden, Pool 3, July to November, 1950, most abundant in July, eggs moderate most of time; Pool 4, Bedford College, Botany Garden, February to November, 1950, scarce until August, when abundant, then scarce in October, never abundant; Pool 5, Botany Garden, 14.10.50., not very numerous, mostly empty, some ephippiate; Pool 7, Bedford College, Botany Garden, July to November, 1950, abundant in summer, males and ephippial females October, and November; Pool 8, Botany Garden, July and August, very numerous; Water Lily Pond, Botany Garden, see appendix 3; Leg of Mutton Pond, Hampstead Heat, 21.10.50., 2 ephippiate females only.

As this species has not previously been recognized there is not published information, concerning it.

My records indicate that it has extremely similar habitat requirements to those of D. obtusa, and I have not been able to detect any reliable ecological differences, except that the present species seems less able to stand low temperatures than does D. obtusa. It probably does not normally over-winter in England.

It appears to be widespread in Eastern England. Scourfield thought that it was mainly found in coastal areas, but this does not seem to be the case. Aldwarke is more than 40 miles from the nearest estuary and 70 miles from the nearest open sea.

Daphnia ~~A~~ambigua

Water Lily Pond, Queen Mary's Garden, 8.8.50., numerous, egg-number 4.6 (4 to 7), 17.8.50., scarce, 25.10.50., abundant egg-number 2.7 (0 to 7) 8.12.50., 3 only, eggs c.2; Island Pond, Queen Mary's Garden, 25.10.50., 1 only.

The few records for this species (Scourfield 1946, Fox 1948, and my own records), give littel clue as to its normal habitat. It is probably an introduced species, but its place of origin must remain unknown, until more tropical waters have been investigated. Such evidence as there is suggests that the species is an inhabitant of small lakes and large ponds. It is clearly a summer form in England, and does not winter.

Daphnia longispina.

Loch on Mor, 4.9.48., abnormal form, abundant; Loch a Phuirt-Ruaith, 7.9.48., very scarce, outside weeds; Lower Greasborough Dam, 30.3.48., 27.48. plankton, very numerous, x.7.48., near vegetation, not numerous; 19.9.48., very numerous, abundant inshore, males; Wentworth Tank, 19.8.49., very scarce; Middle Greasborough Dam, 26.9.50., very numerous, lacustrine type; Outflow, Middle Greasborough Dam, 26.9.50., abundant, some ephippiate, mostly f. Littoralis; John's Trinity Dyke, Cambridge, 8.7.48., not very numerous, ephippiate; Clare Dyke, 26.7.48., extremely abundant; Dyke 448.578., Cambridge, 4.8.48., numerous, males; Ringmere, Thetford, 10.7.48., numerous, one ephippiate; Viaduct Pond, Hampstead Heath, 16.10.48., numerous, some ephippiate, 20.6.49., 24°C, numerous in clear, eggs 3 to 4, some ephippiate, 9.3.5.0., very scarce, clear water, young only, 27.5.50., numerous clear water, scarce weeds, eggs c.6, 16.11.50., one young only; Wanstead Bomb Crater, 25.6.49., very scarce, many eggs; Island Pond, Wanstead, 25.6.49., very numerous eggs low, 16.6.50., abundant, egg-number 3.4; Little Stanmore 1, 9.7.49., scarce, clear water and in Potamogeton; Little Stanmore2, 9.7.49., very numerous, clear and weeds, eggs high, some males, some ephippiate; Warren Pond, 22.10.49., very numerous, c. 6 eggs, 25.3.50., very numerous away from weeds, eggs c.20; Pool W. of Hollow Pond, Epping Forest, 30.10.49., scarce, young only; Badstue Dam, 20.7.50., abundant, eggs c. 15, 30.8.50., abundant, eggs 4.6 (2 to 7); Heskeskoe Dam, 20.7.50., very numerous, eggs c.6; Mörke Dam, Hilleröd, 20.7.50., abundant eggs of most 0 to 10, but one large individual had 30 eggs; Lille Fönstrup Dam, 14.8.50., one only, 5 eggs; Fönstrup Dam, 14.8.50., very numerous, egg-number 6.3 (2 to 8); Deer Paddock, Strödam, 25.8.5.0., very numerous, egg-number 4.0, v.rosea; Hjorte Söle 1, 29.7.50., plankton, very scarce 2 eggs, 25.8.50., very scarce, eggs 0 to 3.

The unfortunate confusion with D. hyalina has made it difficult to interpret the statements of many author's, concerning this species. It seems probable that it may occur in some large deep lakes, Woltereck (1928), but the possibility that all such records merely refer to forms of D. hyalina cannot be excluded. It certainly does not occur in any of the large English or Danish Lakes. Wesenberg-Lund (1926), who was mainly dealing with this species, says that it is most characteristic of the central regions of large pools; Poulsen (1929), says it only rarely occurs in vegetation, and is more common in plant-rich than in plant-poor pools. Pacaud (1939), notes that it does not occur in humic waters. Most authors agree that it is rare in strongly acid waters. Pacaud finds it occurs at pH. 6.0 but is not flourishing; Hubault (1932) and Krasnodebski (1937) have also found it in similar mildly acid waters. Poulsen (1929), states that it is commonest in weakly alkaline waters, but may sometimes occur in strongly acid localties.

On the whole my records support but add little to these observations. The species occupies an ecological zone intermediate between that of D. hyalina, and that of D. pulex. The species are not however separated solely by size of habitat, and the exact species present in any locality probably depends on a complex series of inter-acting factors. Though the species is usually found away from weeds, it does not avoid them so strictly as do other members of the genus. It is of interest that it is also the only member of the genus, which I have found in semi-lenitic habitats. The two records for the Lake District are of interest, since there are not previous certain records; both Wiseen and Wray Mires can be classed either as small lakes or as large pools, and both are shallow.

Most of my localities are weakly to strongly alkaline, but Hjorte Söle is strongly acid (pH. 4.5 to 5.5.) and moreover peaty. A more surprising record is that from Loch on Mor, which is definitely saline, D. magna has commonly been recorded from brackish waters, but I know of no such records for other species of this genus.

My impression is that the species seldom overwinters in England, though Berg (1931) says that it may do so in Denmark. It is noteworthy that it is rare in the true Arctic (Poulsen, 1939, says that it is absent from the true arctic, but it has been recorded from Bear Island (Bertram 1933), and I have seen specimens collected on this island.

Daphnia hyalina

I have found v. hyalina in : Crummockwater, Loweswater, Thirlmere, Buttermere, Crummock Water, and Bure Sö.

I have found v. lacustris, in : Derwentwater, Elterwater, Easedåle Tarn, Drunken Duck Tarn, Regent's Park Lake, the Children's Boating Lake, Regent's Park, the Water Lily Pond, Queen Mary's Garden, a pool in Cripplegate, the Hampton Filter beds, Queen Mary's Reservoir and the Hollow Pond.

I have found v. galeata in : West loch Eilean a Ghille, Loch Druidibeg, Windermere, and the Hampstead Ponds.

Since the habitat of this species prevents adequate collecting in many instances I shall not give any details concerning abundances or seasonal occurence. The species certainly occurs all the year round in Regent's Park Lake, though only in small numbers in the winter. It reproduces even under ice.

So much has been written concerning this, probably the most studied of all Cladocera, that it is quite impossible to summarise it here. The species is generally admitted to be a truly lacustrine form, and is usually considered to be commonest in cooler waters and not very eutrophic lakes. German and Scandinavian workers consider that it is confined to large deep lakes, and it is often treated as an arctic - alpine species (as by Thienemann 1950), though it is not recorded from the true arctic Poulsen (1939, 1940).

These conclusions are not true of England, even when v. lacustris is not considered. They are strikingly untrue if this variety is included. Admittedly this is the only Daphnia common in our large deep lakes, but it is by no means confined to them. It commonly occurs in small, shallow eutrophic lakes and even pools, as my records show. Other workers as Scourfield (1898), and Jenkin (1928), have also recorded it from pools in this country. It is not easy to see why the English distribution of this species should differ so markedly from the European distribution, but it may be noted that consonant differences are shown by D. cucullata, and by Bosmina longispina, and Bosmina coregoni.

Another feature in which English Daphnia hyalina races often differ from those studied on the continent and in America is in the development of the crest. Danish (Wesenberg-Lund 1926, Berg 1931) and American authors are agreed that crests only appear when the water temperature exceeds 12° to 16°C. On the other hand it is well-known that in Windermere galeate and roundheaded individuals with crests are present all the year round (see for instance Scourfield and Harding 1941). Similarly I have usually found v. lacustris with a small crest, even in winter, whilst in the Cripplegate Pool the individuals had very high crests though the water temperature must have been well below 10°C. These facts suggest strongly that, in England at least, Wesenberg-Lund's 'flotation' theory cannot provide an adequate explanation of the function of crests and helmets in this genus.

The individuals which I collected in West Loch Eilean a Ghille, showed an interesting colour variation. Their carapace had a deep brown pigmentation. Such pigmentation is characteristic of arctic races of other Daphnia spp., and it is interesting to find it appearing in S. Uist, the lakes of which form the closest approach to tundra lakes available in low lying areas of the British Isles.

Daphnia cucullata

See appendix 2. Other records are from Hollow Pond, 30.10.49., crest round very low, not very numerous, no eggs; Bastrup Sö, 11.8.50., crest very high eggs c.4;

This species is the common species of the smaller, shallower, eutrophic lakes of central Europe (Wesenberg-Lund 1926, Woltereck, 1928, Berg, 1931, Rylov, 1935 etc.). It is widely distributed in the British Isles (Scourfield and Harding 1941) but it is nowhere very common save in the Broads area (Gurney 1929).

I have discussed it at some length above, and came to the conclusion that the principal features of its ecology are the preference for smallish, shallow lakes, and the need for a rich supply of nannoplankton. Many of the localities from which I have collected in England seem to me to be precisely comparable to localities in Denmark where it flourishes, so that I cannot suggest why it should be so rare,here. The rarity is almost certainly associated with the relative frequency of D. hyalina lacustris in this country. It is noteworthy that high helmeted forms are even rarer than other forms of the species in this country, though very common in Denmark.

Ceriodaphnia reticulata.

Clay Pond, 4.8.49., margin only, very numerous; Drunken Duck Pool, 6.8.49., abundant, many eggs, 27.8.49., abundant mostly in open; Mill Lane Overflow, Cambridge, 4.8.48., scarce; Dyke 448.578., Cambridge, 4.8.48., abundant; Little Stanmore 1, numerous, in clear only, serrata; Little Stanmore 2, 12.10.49., scarce in clear, very numerous in thin weeds, eggs very low; Snaresbrook road, 30.10.49., numerous, eggs less than one, mostly ephippiate; Lower Greasborough Dam 26.9.50., abundant in marshy part, males; Teylgaard Sö, 22.7.50., abundant in waterlilies, numerous in clear water, very numerous in reeds, eggs 2 to 3, v. kurzi; Vilde Ande Dam, Strödam, 25.8.50., abundant, egg-number 2.5 (2 to 4); Badstue Dam 30.8.50., abundant 2.6 (0 to 4); Flats Pool, Hilleröd, 9.8.50., numerous, eggs 2 to 4; Ellessö, 10.9.50., very numerous in reeds, c.40% ephippiate, egg-number 2.7 (0 to 5).

I use the specific name in the sense meant by most European authors, not in that of Stingelin (1913). I cannot agree with his theory that C. dubia is only a variety of this species (see below).

This species seems to be confined to ponds of all sizes and smallish lakes, as Berg has also shown. Poulsen found it normally in vegetation and never in plankton, which also agrees with my experience. My records show that it may occur in somewhat acid localities (Drunken Duck Pool). Passowicz (1935) has also found it in localities with pH. 5.5, but Pacaud (1939) found it only in nearly neutral waters. Pacaud also says that it only occurs in ponds polluted with animal matter. This opinion is directly contrary to my experience, most of the localities where I have found the species being scarcely or not at all polluted.

I can find no ecological distinctions between the races. The strain inhabitating the Drunken Duck Pool makes it somewhat doubtful whether these can be usefully distinguished. It could not be assigned to any of the principal races, and different individuals showed characters of all three in almost every possible combination.

Ceriodaphnia dubia

Ringmere, Thetford, 10.7.48.; Regent's Park Lake, throughout the summer and autumn from June to November, never abundant, becoming very scarce in late autumn, egg-number 12 or more in early summer becoming very low in late autumn, males and ephippial females in authmn; Island Pond, Queen Mary's Garden, 8.8.50., abundant, eggs c.6, 17.8.50., numerous, 25.10.50., scarce, two ephippial, rest empty; Water Lily Pond Queen Mary's Garden, 17.8.50., young, one individual only.

This is the species normally called C. affinis, Lilljeborg. In 1913 Stingelin subsumed this species and also C. limicola Ekman and C. sylvestrii Daday under C. dubia Richard. This he treats as a variety of C. reticulata, but, as Gurney (1927), has shown, this is undoubtedly incorrect. Gurney agreed that C. affinis etc., must be placed under C. dubia. Somewhat reluctantly I feel bound to agree with this, as I can find no reliable differences between these species. Whether all forms recorded as

C. dubia are identical is another question. That of Sars (1916), for instance, definitely lacks the characteristic comb on the claw.

Wagler (1936) treats *C. affinis* as a variety of *C. quadrangula*. This is certainly incorrect. *C. dubia* is a much larger species than *C. quadrangula*; the head is more like that of *C. reticulata* than that of *C. quadrangula*, the post-abdomen is larger, has more numerous anal denticles and is straight, not concave, behind them. The claws of *C. quadrangula* completely lack the 'affinis' comb, and the carapace markings are much more distinct. Intermediates are not recorded.

The key of Scourfield and Harding (1941) is misleading in respect to this species. It is joined with *C. quadrangula*, in opposition to *C. pulehella*, as having the head not inflated in front of the antennules. In fact the head is usually somewhat inflated, and may be quite as much so as in many individuals of *C. pulchella*.

In view of the controversy concerning this species I am including figures of specimens from Regent's Park Lake (Figs. 8 and 9.)

Little seems to be known about the biology of this spcies which seems to be rare everywhere in Western Europe. On the other hand it appears to be rather common in warmer regions, judging by the large number of published records. It has an immense longitudinal range, being found from Patagonia to Sweden. The records show that it is generally a lacustrine form, and Scourfield and Harding (1941) give it as inhabiting the same sort of localities as *C. pulchella*. My localities, small lakes and large pools, with rich plankton, agree well with this distribution. It is not normally found amongst weeds.

Ceriodaphnia quadrangula

Pool near Loch Ness, 16.6.50.; Hjorte Söle 2, 29.7.50., numerous, eggs c.1 (0 to 2); Storre Gribsö, 3.8.50., plankton very abundant eggs c$\frac{1}{2}$ .9, very small; Bönderness Mose 1 and 2, 3.8.50., very abundant, eggs c.3; Bonderness Mose 3, 3.8.50., very numerous, eggs c.2;

I regard this species in the usual restricted sense and not in that of Wagler (1936).

This species is accepted by all authors to be planktonic. It is also generally regarded as occuring principally in highly acid waters, where it replaces *C. pulchella*, both as a lake plankton, and as a pond form (Poulsen, 128, Scourfield 1903, etc.). My records all agree with this distribution. If these two species are really distinct then it must be presumed that *C. quadrangula* is restricted to acid waters by competition. It is possible however that the two forms are merely ecophenes.

Ceriodaphnia pulchella.

This is one of the commonest species of Caldocera. Since I have nothing to add to the accepted views on its ecology, I shall not give my numerous records in full. I have found it in one locality in S. Uist, the Hill Pool at Loch Skiport; in all 7 small lakes and large pools I have collected in S. Yorkshire; and one small pool, Lower Thrybergh Dam; in 4 of the richer tarns, Blelham, and Windermere, in the Lake District; in 6 large pools and 2 small pools, in Queen Mary's Garden, in London; in 13 large lakes and pools, in Zealand; and in 3 lakes and one large pool in Jutland. Several of these localities are slightly acid, as the Loch Skiport Hill Pool, and the Ugl Sö, but none are very acid, and most are markedly alkaline, 'evolved' lakes and pools. I have found the species throughout the year from March to September but never in Winter.

These records agree with the general opinion that this species is characteristic of lakes and pools, particularly large pools which are more or less alkaline and rich in nutrients. The species is also generally regarded as a summer form.

Wagler (1937), treats this species as a variety of *C. quadrangula*. Whilst I am not convinced that the two species are really distinct, I prefer to follow the majority of authors in treating them separately, for convenience.

The strain of *C. pulchella*, occuring in the Badstue Dam was of interest, since it belonged to the variety *pseudohamata*, which parallels, *C. quadrangula v. hamata* in the development of its fornices. Whilst this last seems to be rather common, *C. pulchella v. pseudohamata* seems to be distinctly rare.

Ceriodaphnia megalops

Blelham Ic, 4.8.49., numerous; Blelham Ib, 18.8.49.; Blelham IVa, 8.8.49., numerous; Blelham Outflow, 8.8.49., numerous, especially at the margins; Drunken Duck Pool, 27.8.49., numerous eggs c.10; Little Stanmore I, 9.7.49., scarce in clear water, very numerous in *Lemna*, very scarce in *Potamogeton*, 12.10.49., very scarce in algae mats and thick weeds, no eggs; Little Stanmore II, 12.10.49., very numerous in thin and thick weeds, eggs very few, mostly 0 but some to 7, some ephippiate; Warren Pond, 22.10.49., abundant, eggs low, many ephippiate; Teylgaard Sö, numerous in and near weeds, eggs c.5; 2.9.50., one only in reeds, 9 eggs; Fönstrup Dam, 14.8.50., very scarce eggs two; Karlssö, 19.8.50., one only, 5 eggs.

The published descriptions of this species are misleading. The post-abdomen is usually described as incised proximal to the apex. This is true of preserved animals and of animals compressed under a coverslip, but it is a result of the contraction of the anal muscles. In the relaxed post-abdomen there is no incision. In my experience this may cause difficulty to the beginner.

My records suggest that this species, though somewhat less common, occurs in the same type of habitat as <u>C. reticulata</u>. This is borne out by published records. All western European authors (as Poulsen 1928, Berg, 1929, Jenkin 1928, and Pacaud, 1939) are agreed that this species is almost always found amongst thick vegetation in small waters. Berg states that he has never found it in the littoral region of lakes. It is however clearly established in Blelham Tarn, and it is also recorded from Windermere, and Esthwaite Water (Scourfield and Harding 1941). The rarity of both this species and <u>C. retirculata</u>, in large lakes, is probably due to the scarcity of suitable habitats, rather than to anything deleterious in the general character of such lakes.

Pacaud and Poulsen find the species mainly in alkaline habitats, but it is recorded from acid localities by Berg. Only one of my localities is markedly acid, but this is sufficient to show that there is no restriction to non-acid localities in England.

Apart from the difference in food which I have already noted in section 3, I can find no differences in ecology between this species and <u>C. reticulata</u>.

Ceriodaphnia laticaudata

Stilligary Ditch, 3.9.48., abundant, one ephippiate; North Ings, Mexborough, 20.8.48., very scarce; Aldwarke Marsh, 16.8.49., in Typha, numerous; Upper Thrybergh Dam, 18.8.48., very numerous, 29.9.50., very scarce; Hampton Long Water, 26.2.49., very scarce; Bomb Crater, Wanstead, 25.6.49., numerous; Island Pond, Wanstead, 25.6.49., not very numerous; Flats Pool, Hillerød, 9.8.50., abundant, eggs 2.2 (0 to 5), ephippial females and males; Sorte Dam, Strødam, very numerous, egg-number 1.8, (1 to 2), males.

This species is often considered to be rare, but it is more probable that it is usally overlooked because of its peculiar habitat. Most workers who have found this species at all often are agreed on its principal requirements of thick, rich, decaying vegetation (Berg, 1929, Pacaud 1939, Scourfield and Harding 1941), though Birge (1918), merely gives its habitat as amongst weeds. As a consequence of this habitat preference it is of course rarely found in large lakes, though it has been recorded from a particularly swampy portion of the shores of Windermere (Borran's Field). My experience is in complete agreement with the experience of previous workers. These do not however, stress one important feature, that the individuals of this form are most usually to be found actually burrowing in masses of decaying vegetable matter. Pacaud notes the close parallel between the habitats of this species and those frequented by C. rotunda; this is very striking, but I find C. laticaudata to be considerably more catholic in its choice of habitats.

Ceriodaphnia rotunda

Fønstrup Dam, 14.8.50., two, 2 eggs; Praestevang I, 1.8.50., scarce, c.3 eggs.

This species is very seldom recorded, and most authors (as Keilhack, 1909) consider it to be very rare. Pacaud (1939) suggests that it is not really rare, but has been overlooked, because of its restricted, and peculiar habitat. He has found it not uncommonly in France. There is probably some truth in this contention, but even when allowance is made for the difficulty of discovering it, I think it must still be classed as a rare species. It is for instance much less commonly found than C. laticaudata and Ilyocryptus sordidus, which are just as likely to be overlooked.

Pacaud claims that it is only to be found burrowing in the thick deposits of black ooze produced by the decay of plants and especially Lemna. All other authors have contented themselves with saying that it is found amongst weeds; but Pacaud is almost certainly correct. My two habitats correspond exactly with Pacaud's designation. It is particularly noteworthy that the species only occurred in those parts of the pond where the Lemna detritus was already finely divided, not amongst the thick deposits of decaying but still identifiable Lemna plants.

The species has only been recorded from a few other Danish localities (Berg, 1929), and there is no certain English record (Scourfield and Harding 1941), but it seems likely that if search is made in suitable localities it will be found in more areas in both these countries.

Ceriodaphnia setosa

Praestevang 1, 22.7.50., abundant, 2 to 4 eggs, 1.8.50., very scarce, c. 3 eggs; Vilde Ande Dam, Strödam, very scarce, one with 4 eggs, one ephippiate.

It seems probable that this species is the same as C. acanthina Ross, a North American species. Apart from the slightly longer antennules of *C. setosa* I can detect no reliable differences between them. Unfortunately *C. acanthina* has priority. However, since *C. setosa* is so well established in the European literature, I prefer not to abandon the name, without seeing actual specimens of *C. acanthina*.

The species is even more rarely recorded than the last and nothing reliable is known of its ecology. Statements in the literature are of the same order as that of Scourfield and Harding (1941), 'rare, always amongst weeds.'

My records are the first records for Denmark. The species seems to be strictly confined in these two localities to the thick masses of decaying *Lemna*, in which it burrows. Unlike *C. rotunda* it is not found in the adjacent ooze. If, as seems probable, this is its normal habitat it will normally be overlooked, unless it is extremely abundant, since partly decayed *Lemna* is the most difficult of all materials to search thoroughly. Thus, like *C. rotunda*, it is probably much more common than the very few records indicate.

It may be noted that from an ecological viewpoint these last three species of Cladocera form a distinct group with almost but not quite identical habitats. Of these the most catholic (*C. laticaudata*), is also the commonest, whilst the two more specialized species are distinctly rarer.

Simocephalus vetulus.

There is no point in giving a full list of my records for this, the second most frequent of all Cladocera in western Europe, and I will only give a condensed account. I have only 1 record from S. Uist, Howmore Pool. I have records for a pool near Loch Ness; for Wharton Tarn, and Windermere in the Lake district; for a pool in Malham Fen; for two small ponds and

Lower Greasborough Dam, in S. Yorkshire; from the river Cam and 11 other localities at Cambridge, several of them semi-lenitic; for Ringmere, Thetford; for 20 localities in London, one semi-lenitic; for nine lakes and ponds in Zealand; and for one lake, Borressö, in Jutland.

The species is well-known to occur almost every where both in pools and lakes where there is rather but not excessively thick vegetation, and as was to be expected most of my habitats are of this sort.

Poulsen suggests that it is mainly a species of alkaline waters and is replaced in slightly acid waters by S. exspinosus, whilst Harnisch (1929) makes the amazing statement that the members of the genus Simocephalus, do not occur in bogs (see S. serrulatus below). Pacaud (1939) on the other hand records the species as being common in slightly acid waters. Unfortunately, as I have noted above there is reason to believe that he confuses the two species S. vetulus and S. exspinosus. Whilst I have no records from a very acid locality I have several from localities with soft water which must be slightly acid at times (e.g. Wharton Tarn, Windermere). I have numerous records of S. exspinosus, from localities with very hard water. I find it impossible to agree with Poulsen, and think that these two species have precisely similar habitat requirements, except in respect of food-supply (see above.)

It is interesting that in small woodland pools, species of Simocephalus may occur in the complete absence of vegetation, provided that there are many dead leaves. I found S. vetulus in such a pool in Denmark (in Praestevang), and I have a similar record for S. exspinisus, from Brathay Quarries, Lake District. Daphnia species are not common in these small woodland puddles, which are almost choked with leaves, and it is possible that Simocephalus survives there owing to absence of competition.

Pacaud notes that S. vetulus does not occur in pools that are more than slightly polluted. In my experience this is true of all species of the genus. I never find them in typical 'Daphnia' ponds, and the only locality known to me in which this species occurs with Daphnia obtusa, is a remarkably unpolluted habitat for that species (the Newt Pond Putney Heath).

Simocephalus exspinosus

For this species, as for S. vetulus, only a summary of my records is necessary. I have found it in 4 pools in S. Yorkshire; one dyke at Cambridge; in 11 localities, both lakes and pools in the Lake District; in 8 localities in London; and in 7 ponds in Zealand.

These localities ranged from slightly acid to very alkaline (e.g. Bedford College Botany Garden, Frederiksborg Slotssö).

It is possible that this species withstands pollution better than S. vetulus. I have three records for 'Daphnia' ponds (the Leg of Mutton Pond, 2 ponds in the college Botany Gardens). I have also two records from 'foul' Lemna ponds (Praestevang 1, and the Vilde Ande Dam). The records suggest that it may prove to be more resistant to low oxygen tensions than S. vetulus but I have no experimental data to prove this.

Apart from this the only difference in ecology that I have been able to detect is in their food. S. vetulus is principally a detritus feeder, whilst S. exspinosus is principally an algal feeder.

Simocephalus serrulatus

Loch a Phuirt-Ruaith, 7.9.48., very scarce; Hjorte Söle 1, 29.7.50., very scarce, margins only, eggs c.2, 25.8.50., scarce, margins; Hjorte Söle 2, 29.7.50., very abundant, egg-number 4.5 (3 to 6); Storre Gribsö 3.8.50., I, very scarce, young only, II numerous eggs c.6, IV, scarce, eggs low;

Lille Gribsö, 3.8.50., II one young only; Mörke Sö, Silkeborg, 11.9.50., very abundant, at margins amongst vegetation only, many eggs.

As other species of this genus, S. serrulatus is normally found in thick vegetation, though it is evident that sphagnum may be satisfactory. It is quite impossible to reconcile other statements made by authors concerning this species. Birge (1918) says that in North America it is common everywhere amongst weeds, and is the most abundant species of the genus. This is certainly not true in Europe. Pacaud (1939) and Litynski (quoted in Pacaud) regard it as occurring mainly in places very rich in humic detritus. None of my localities correspond with this description, and my food records (of small Algae) do not suggest that such detritus would be of any importance. It seems unlikely that the species is found often in such places in England and Denmark, and I have certainly never found it in them. Scourfield and Harding say vaguely that it occurs in small weedy water,s, and is rather rare. Even this statement is open to exception, as Loch a Phuirt-Ruaith, and Storre Gribsö can scarcely be called small waters.

Poulsen (1928) has only found it in a few strongly acid localities, mostly with spagnum. Berg (1929) also found it in four localities, (two of which, Storre Gribsö, and Hjorte Söle, are the same as mine) all of which had brown stained water and some sphagnum near the margins. Hjorte Söle is a typical bog-lake. Passowicz (1938) also finds it in peat pools with pH.5.4 to 5.5, though Pacaud failed to find it in such localities.

The German Sunda expedition collected specimens of this species from a Sphagnum pool near Lake Toba, with a pH. of 4.3; but also in the plankton of a Sumatran lake with a pH. of 8.4. Brehm (1933) who records these, considers the last record to be very unusual, and regards the species as characteristic of the littoral region of acid waters.

My records are all from acid waters, and all my localities could be considered dystrophic, to a certain degree, with the exception of Loch a Bhuirt-Ruaith, which is more or less oligotrophic. It seems definitely established that the species is confined to strongly acid waters in Denmark, and these are probably a principal habitat in many parts of its range. Such a conclusion is equally obviously untrue when applied to the species as a whole, and the problem needs much further study. The results obtained up to the present moment strongly indicate that this species comprises a number of biological races, each of which is restricted to a definite sort of habitat by competition with the other species of the genus, but which together are able to range over almost the whole series of habitats that the genus can occupy.

Scapholeberis mucronata

As with the two common species of *Simocephalus*, I do not intend to give full records of this species, for which I have more localities than for any other species except *Chydorus sphaericus*. I have records from 3 pools, and from Lower Greasborough Dam in S. Yorkshire; from thick reed beds in Windermere and Belham Tarn in the Lake District; from 9 dykes and pools in Cambridge; from Fowlmere Pool, Thetford; from 14 small and large pools in London; from 15 small lakes and pools, and 3 large lakes in Zealand; and from two lakes and two pools in Jutland.

In all the larger habitats I only found the species in thick reed-beds or amongst dense floating vegetation in sheltered bays.

Scourfield (1896, 1900) has drawn attention to the peculiar structure of this species, and its habit of clinging to the surface film.

This behaviour is readily shown by animals in the laboratory. One would expect from this that the primary limiting factor in its distribution would be the need for a reasonably smooth and undisturbed water surface. Thus it would be able to live in open water in small sheltered localities, but would be confined to sheltered weedy waters in large lakes. My records show that this is so.

The species is common in very acid waters (e.g. Hubault, 1932, Krasnodebski 1937, Pacaud 1939). Certain authors, as Naumann (1929) think that highly alkaline waters are unfavourable to this species but Poulsen (1928) finds it in waters which are strongly alkaline as frequently as in waters which are acid, and Pacaud (1939) records it from a pool with a pH of over 8. My records also suggest that this species is almost completely independent of pH, occuring equally in highly acid bog-pools such as Hjorte Söle 2, and the pools in Bonderness Mose, in neutral waters, and in pools such as the Jaegerbakke Dam which are very hard and may have a very high pH.

It is possible that in the past this species has been confused with Scapholeberis kingi, which has only recently been recognized as a European species (Rammner 1929, Poulsen 1928). I am certain that all my specimens belong to S. mucronata since they completely lack the characteristic carapace sculpture of S. kingi. The confusion has probably not led to many errors concerning the ecology of the species since that of S. kingi seems to be very similar, to judge from published statements such as those of Brehm (1933).

Moina macrocopa

Aldwarke Wash, 24.9.47., abundant, 2.8.49., very abundant, 4.6.49., very scarce, 2.8.49., abundant, 11.9.49., many ephippiate, 10.10.49., very scarce, 3.7.50., extremely abundant, many ephippiate; and on other occasions in warm weather.

Though attempts have been made by Brehm (1933), and Jenkin (1934), to arrange certain sections of the genus, the systematics of Moina are still in a state of chaos; and it is often difficult to be sure of the identity of collected specimens. Judging from Brehm's account, Moina macrocopa is one of the most distinctive species. The only species with which it is likely to be confused are M. belli Gurney, and M. banffyi Paday, and it is possible that both of these are only varieties of M. macrocopa. M. belli is an African species, not recorded nearer to the British Isles than N. Africa and Crete. It should be identifiable by the ciliation of the dorsal margin of the head, also present in M. banffyi which is perhaps synonymous. It seems safe to ignore it unless should be strong grounds for suspecting that any specimens belonged to it. M. banffyi is only known from Hungary and the Isle of Wight. Scourfield and Harding do not include it in their key, since they regard it as synonymous with M. macrocopa. According to Brehm's character summary it is characterised by having the dorsal margin of the head thickly covered with hairs. The antennae and antennules are also very hairy, and the latter are squamous.

My specimens correspond exactly with the published descriptions of M. macrocopa, and do not show any of the peculiarities of M. banffyi.

This species is widely distributed occuring in Central Europe, Central Asia, Japan, the warmer parts of N. America, N. Africa, and S. Africa (Brehm, 1933, Birge, 1918). It is, however, rarely recorded. The distribution is dominantly southern and its most northerly known localities are in England. Scourfield and Harding (1941) state that it occurs in small ponds, is rare and is confined to the S. and E. of England and S. Wales. Recently Galliford (Harding in litt.) has found specimens in the Leeds and Liverpool Canal, Lancashire. This locality and mine are thus the two most northerly known habitats of the species, in the whole world.

In Western Europe *Moina* spp. are confined to small ponds, though rare in temporary ponds (Berg, 1929, Pacaud 1939, etc.). In the tropics, planktonic species occur, and, outside the tropics, species have been found in the plankton of exceptional lakes, such as those with very high magnesium content (Hutchinson 1933), or with high salinity, such as the Aral See (Rylov 1935). Many such records are for the present species or forms thought to be synonymous with it. Berg (1931) regards the restriction of *Moina* spp. to small ponds, in Western Europe, as a consequence of their need for high temperatures. On the other hand Pacaud (1939), thinks that considerable quantities of suspended silt are an essential factor. There is probably some truth in both of these contentions, but even together they do not fully explain the facts of *Moina* distribution. Indeed almost the only feature common to all the habitats of these species in temperate regions, is that they are all in one way or another extreme habitats for Cladocera. It is noteworthy that the habitats in which *Moina* is most commonly found are those which are least characteristic of most species of *Daphnia*. In my two *Moina* localities the *Moina* is never abundant at the same time as the associated *Daphnia* species. I would suggest that *Moina* species are almost confined to the most turbid and warmest localities in Western Europe, because it is only in these localities that they can compete successfully with *Daphnia* species.

Aldwarke Wash is a good example of such an extreme habitat, in which there is nevertheless a good food-supply for those species which can survive. It is a shallow expanse of water several acres in extent, but with a maximum depth of c.40 cms. in winter and c.20 cms in summer. It is bounded on one side by a sewage works, and on another by a steel works tip, so that it is very highly polluted. The bottom is formed of a thick layer of black, sulphureous mud containing thousands of Chironomid larvae. There is usually an abundant supply of small flagellates. The temperatures may become very high indeed during the summer months. The extreme character of the locality is reflected in the monotony of the fauna, though the number of individuals present may be very high. Besides those already mentioned, the only forms I have seen are : *Daphnia curvirostiris* (see above), a species of mosquito larva, an eristalid larva, *Chydorus sphaericus* (in the winter only), a species of Cyclops (in the winter only), enchytraeids, and *Hydatina senta* (in the winter only).

Moina rectirostris

Witt's Farm, ~~God's Hill~~ Godshill, Hampshire, 8.6.50., very numerous, eggs c.15.

My specimens agreed in every detail with the published descriptions of this species. Males and ephippial females were produced in the laboratory, and also agreed perfectly with *M. rectirostris*, so that there can be no possibility that they belonged to *M. brachiata* or *M. affinis*, the only other species which they at all resembled.

In the British Isles the species is less rare than *M. macrocopa* but is also confined to England and Wales (Scourfield and Harding, 1941). It is still a distinctly rare species. Like *M. macrocopa* it is confined to small turbid ponds, but it is more northerly in its distribution, reaching to S. Sweden.

My remarks concerning the ecology of M. macrocopa are equally applicable to this species. It may be noted in addition that the records for this species indicate that it is strictly confined to alkaline waters. This is probably also true of M. Macrocopa, but the records for that species are too few for such a statement to be reliable.

Bosmina

The systematics of this genus are more confused than those of any other Cladoceran genus, and it seems unlikely that a reliable classification will be produced for many years. All authors recognize two groups of species in Europe, the B. longirostris group, and the B. coregoni group. Almost all authors further agree that the forms of the former group are merely varieties of one species. The number of species recognized in the latter group varies considerably from author to author. Most recent European authors recognize only one species divided into numerous subspecies, races, and forms (e.g. Rylov 1935). Scourfield and Harding (1941) recognize no less than 5 species. I find it quite useless to attempt to differentiate all of their species, but on the other hand I am unwilling to treat them as one species. On the basis of general form Rylov (1935), recognizes two series of varieties, the 'longispina' series, and the 'coregoni' series. I propose to treat these as two species since they differ also in geographical distribution, though their ranges show a very considerable overlap, and in ecology. Bosmina longispina includes not only this species but also B. obtusirostris (a later name); whilst B. coregoni includes the other three species of Scourfield and Harding.

Bosmina longirostris

There is no purpose to be served by giving all my records for this extremely common species. I have records from three ponds and the two Greasborough Dams in S. Yorkshire; from Tarn Hows, Blelham Tarn, and Elterwater in the Lake District; from 17 small and large ponds in the London area; from 8 ponds and small lakes, Esrum Sö, and Bastrup Sö, in Zealand; and from Madum Sö and Ellessö inJUtland.

The species is generally accepted to be characteristic of small lakes and ponds, and to be frequent in their plankton (Berg 1931, Pacaud 1939 etc.) Poulsen (1928) notes that it may occur in vegetation, though normally planktonic. Wesenberg-Lund (1904), notes that it may occur sometimes in the plankton of larger lakes. Both Pacaud and Poulsen note that the species is most frequent in alkaline waters, though it may occur in acid waters. Pacaud notes that he is unable to find any correlation between the pH. of a locality and the morphological or of this species occuring there.

My experience is in agreement with these records. The species is frequent in ponds of all sizes provided that these are alkaline and not too highly polluted. It is also frequent in small lakes where these are alkaline or only slightly acid. I have sometimes found the species amongst vegetation, but, wherever I have had plankton samples also, it has been more abundant in the plankton.

In England it tends to be replaced by *B. longispina* both in large lakes, and in small slightly acid lakes and slightly acid large pools. The two species are seldom found together (in the Lake District the only lakes from which both are reliably reported are Esthwaite Water, and Grasmere), and then only in lakes of medium size. The ranges of the two species are probably largely determined by competition, *B. longispina* being favoured by large habitat size and *B. longirostris* by more alkaline water. That large size of localities, and acidity, are no absolute bar to *B. longirostris* is shown by its occurence in Esrum Sö, and Madum Sö. The former is larger than any English Lake; whilst the latter has an almost constant pH. of about 5.

Bosmina longispina
including *B. obtusiroatris.*

Loch Ness 23.6.50., very large; near Loch Ness 16.6.50., brown carapace pigment, 22.6.50., 27.6.50.; Pool; Red Tarn, Helvellyn, 4.8.49., abundant, many eggs, brown carapace pigment; Windermere, inshore in small numbers on 8.8.49., and 12.8.49., in North Basin, numerous, few eggs, 24.8.49., in S. Basin plankton, 30.8.49., not very numerous, eggs high; Derwentwater, 24.8.49., abundant, many eggs; Crummock Water, 24.8.49., very numerous; Lake Bassenthwaite, 24.8.49., scarce; Easedale Tarn, 15.10.49., scarce; Queen Mary's Reservoir, 25.6.49., very abundant, f. *lacustris*; Almind Sö, 11.9.50.

I have already discussed the differences in ecology between this species and *B. longirostris.* There are also marked differences in ecology between it and *B. coregoni.* *B. longispina* is commonly considered to show an arctic-alpine pattern of distribution (Rylov 1935, Thienemann), whilst *B. coregonis* is though to be more southern, and is common in the lakes and large ponds of the central European plain. The geographical distinction is not absolute even in Europe, but on the central plain *B. longispina* is rare and restricted to large deep lakes (Wesenberg-Lund 1904, Berg 1929, etc.) whilst *B. coregoni* is found in a wide range of eutrophic lakes and ponds, often with *B. longirostris* (Berg, 1929). *B. longispina* may occur in eutrophic lakes of large size, but it is more characteristic of oliogotrophic lakes, or at least mesotrophic. On the whole my collections accord well with these opinions of European authors, though their opinions concerning *B. coregoni* are not completely in accord with its ~~E~~. British distribution (see below.)

Bosmina coregoni

I found this species in Bastrup Sö, Arressö, Ugl Sö, and Almind Sö, in Denmark. I would probably have found it more frequently had I been seriously collecting plankton. I have never found it in England.

It is of interest that two of these lakes are slightly acid according to the Hilleröd staff, though both also contained *D. cucullata*. The record of both *B. coregoni* and *B. longispina* in the **same** collection from one of these (Almind Sö) is of interest.

Bosmina coregoni, though widely distributed is distinctly rare in the British Isles (see for instance Scourfield and Harding, 1941). Thus it is not very surprising that I have not found it there. On the other hand it is the commonest member of its group on the central European plain. I have collected in a number of habitats that would appear suitable to it without success. This distribution of these two related species recalls the distribution of *D. hyalina*.and *D. cucullata*. A difference is that *Bosmina longispina*, unlike *Daphnia hyalina* does not show a greater range of habitats in England that it does in Europe. Unfortunately there seems to be no obvious explanation of these anomalies in the English distributions of planktonic Cladocera.

Ophryoxus gracilis

Loch Ness, 23.6.50.

This extremely rare Cladoceran is only known in the British Isles from Loch Ness, Loch Oich, and the intervening portion of the Caledonian Canal. It is a sub-arctic species and these are its most southerly localities in Europe.

It is a weed-dwelling species (Birge 1918), but little seems to be definitely known of its ecology. The fauna associated with it in my collection suggest that it has habitat requirements similar to those of *Sida crystallina,* which does not seem to occur in Loch Ness. As I have pointed out in part 1, this is one of the very few Cladoceran species in which temperature seems to be the most important factor determining the distribution, though this has not been checked experimentally.

Ilyocryptus sordidus.

Wray Mires II, 24.8.49., scarce; Druhken Duck Tarn, in mud, 27.8.49., scarce, Low Wray Bay, Windermere; Upper Ravenfield Dam 28.8.49., scarce; 30.8.49., scarce; Fowlmere, Thetford 10.7.48.; Children's Boating Lake, Regent's Park, 26.10.48., scarce, 30.1.50., scarce, eggs c.4, 18.11.48., scarce, 14.7.50., scarce, 12.10.50., very scarce eggs c.5; Regent's Park Lake, 1.3.50., numerous, eggs c.5, 28.3.50., numerous eggs c.6, 24.4.50., numerous, eggs moderate, 28.4.50., Bridge 2, scarce, eggsc8, 8.5.50. very numerous, some even at surface in floating debris, 15.6.50., numerous, eggs c.9; Water Lily Pond Queen Mary's Garden, 29.3.50., very numerous, 3 to 4 eggs, 12.5.50., very numerous eggs c.5, 24.6.50., numerous, eggs moderate, 18.10.48., scarce, 26.10.48., very scarce, 29.4.49., scarce, 23.1.50., numerous; Diana Pond, Bushey Park, 12.1.49., scarce; Highgate I, 21.2.49., muddyish margin, very scarce; Highgate IV, 13.5.50., in reeds, scarce; Connaught Water, 25.3.50., numerous eggs 4 to 6; Warren Pond, 25.3.50., in rushes one young only.

This species is not often recorded, but this is probably a result of its burrowing habits, which are well-known (Wesenberg-Lund 1939, etc.). Berg (1929) and Scourfield and Harding (1941) think that it is really not uncommon. Lilljeborg says that it is not found near the shores of lakes but may be found in depths of 40 to 60 metres. However Berg has found it in small localities in shallow water and most English records seem to be for such habitats. Whilst it is well-known to be a burrowing species, I can find no opinions as to the sort of mud in which it burrows.

My collections indicate that the species is only to be found in a very well-defined type of habitat. It lives burrowed in soft flocculent, brown lake mud, which is not greatly de-oxygenated, and it is also only abundant where there is a supply of small algae either in the mud or in the overlying water. Such deposits are characteristic of depths of from $\frac{3}{4}$ to c.3 metres in small eutrophic lakes, and may also occur in patches in less eutrophic small lakes. Whenever I have been able to obtain adequate collections from such muds I have always found the species. In Frederiksborg Slotssö and Karlssö, Hillerød, the bottom is largely of this type and the species ought to occur. Though I was unable to find it myself, it has in fact been recorded from both lakelets. With the exception of the collections from the Children's Boating Lake, all my records of this species away from such habitats are for localities which do in fact contain such habitats, so that my specimens, always few in number, were probably wanderers from the main population. The bottom of the Children's Boating Lake is formed by thick deposits of living and dead Algae, cast carapaces of Cladocera, and vegetable detritus. Though chemically different from true lake mud this has much the same the texture. Thus it is possible that it is the physical character of the mud, and not its chemical nature, which is of most importance.

The rarity if this species in the littoral region of large lakes is easy to understand in view of the rarity of suitable deposits of mud, whilst it would probably be expected in the bottom muds of deep water, provided the hypolimnion contained a fair supply of oxygen. Thus this concept of the e cology of the species reconciles the observations of Berg and Lilljeborg.

Ilyocryptus agilis

Granta Inn Pool, 26.7.48., numerous; Log Sö, 5.8.50., III, scarce, no eggs, IV, numerous 0 to 2 eggs; Jaegerbakke Dam, 30.8.50., very scarce, one with 8 eggs.

This is less strictly a burrowing form than I. sordidus. Scourfield and Harding (1941) say it is rare, and occurs in mud and amongst weeds, and this adequately sums up current opinion. My records are from silty rather than truly muddy places, always near to weeds. I have never found it in a typical I. sordidus habitat.

Macrothrix laticornis

West Ditch, Coldham Common, 2.5.7.48., scarce; Coldham Brook, 25.7.48., scarce; Hampstead 1, 1.11.48., very numerous, one ephippiate, 27.5.50., scarce eggs 2; Hampstead 2, 1.11.48., scarce; Hampstead 3, 12.11.49., open bottom and cut reeds, scarce, eggs 1 to 2, 9.3.50., open bottom, numerous, eggs 2, 27.7.50., not very numerous in open, very numerous in weeds, eggs c.6; Highgate 1, 13.5.50., scarce, eggs c.5, 5.7.50., very scarce eggs 2; Highgate 2, 13.1.50., away from margins, scarce, eggs 2; Vale of Health pond, Hampstead Heath, 16.10.50., very numerous, eggs c.2; Viaduct Pond, Hampstead Heath, 16.12.50., very numerous, mostly young or empty; Hampton Wick Pool, 3.2.49., under ice, very numerous; Hollow Pond, 23.2.49., numerous at margins; Warren Pond 22.10.49., very numerous, 25.3.50., numerous, eggs c.5; Connaught Water II, 25.3.50., not very numerous, eggs c.4; Newt Pond, Putney Heath, 24.3.49., scarce, only away from weeds; Hadley Wood 'Lake', 23.5.49., scarce.

Poulsen (1928), gives this species as occurring in mud, a record which I find it impossible to reconcile with my findings. Scourfield and Hading say it is widely distributed but not common, occurring at the margins and bottoms of ponds and lakes, especially those of a sandy nature. Berg (1928), also considers that the species is rare.

My records shown that in the London area at least it is anything but rare. They strongly confirm the opinion that the species is most often found in localities with a sandy bottom. Indeed I consider this to be one of the principal features in the ecology of the species. Almost all my specimens were taken over a bottom of sand consolidated with a little silt. Sometimes as at Hampstead 3, and Connaught water I have taken a few individuals over bottoms of pure silt, but in all these cases the species was more common on adjoining patches of pure sand. In dealing with these bottom species it must be remembered that it is the micro-habitat which is important. A habitat as a whole may be characterised by silt or mud but contain isolated patches of more sandy material on which M. laticornis individuals congregate. It is thus possible that Poulsen's muddy localities did not after all differ very fundamentally from those in which I have found the species.

Pacaud (1939) considers that this species, does not occur in waters with a high calcium content, nor in dystrophic waters. The latter statement may well be true, but the first is definitely untrue. The various pools on Hampstead Heath all have distinctly hard, though not very hard water, and the same is probably true of my other localities. It may be suggested that the real restricting factor in Pacaud's localities also, was the nature of the bottom deposits, since sandy bottoms will tend to be uncommon in pools with a high calcium content, in most districts. The large number of pools with hard water and sandy bottoms in the London area is certainly an unusualy feature.

Whilst consolidated sand seems to be the most favourable habitat for this species, loose sand is definitely not a usual locality. I have never found a single specimen on the stretches of loose coarse sand, common in lakes.

Macrothrix hirsuticornis f. arctica G.O. Sars

Apus pond, ~~God's Hill~~ Godshill, Hants, 31.10.49., very scarce, eggs 15 to 24+, length 1.5 mm;

Macrothrix hirsuticornis, which includes *M. arctica*, G.O. Sars, and in my opinion also *M. propinqua* G.O. Sars, is common in the arctic and antarctic, rare in temperate regions, and extremely sporadic in the tropics (Parenzan, 1942). The form *arctica* is the only form found in the Arctic, but is only very rarely reported from temperate countries (Berg 1933, Parenzan 1942). In the arctic it occurs in both lakes and pools, and may be very abundant, as it was in my Bear Island material. Berg's record is for a small temporary pool.

I have not found the typical form of this species, but I have been fortunate enough to collect specimens of *f. arctica* which has not been previously recorded from this country. My specimens (figs. 10 to 13) agreed in most features with those described by Berg, but differed in a few unimportant details. The groups of anal denticles were even more numerous than in his form being c.12 in number. The abdominal setae were setose for 50% of their length (fig. 10). In size they were even larger than the largest populations of f. *arctica* of which I have seen records some of my specimens reaching 1.8 mm. in culture. The antennules differed slightly from those usually recorded for the species, since they had only 4 to 7 instead of 6 to 9 lateral rows of setae on the anterior margin (fig. 13) but this difference is not sufficiently important to affect the identification. I obtained a number of males in culture, which appeared to agree in all characters with those described by Berg. The male of the typical form has never been described.

Berg regards f. *arctica* as merely a luxuriant form of *Macrothrix hirsuticornis*, developed under good conditions. In view of its sporadic occurrence in temperate countries, this view is tempting, but it cannot easily be reconciled with the constancy of characters which the form exhibits in culture, even when no particular care is taken to ensure good conditions.

My locality and that of Berg are remarkably similar, both being grass -bottomed temporary ponds with at the most slight pollution. In both ponds the species was associated with Chirocephalus. The Branchiostracan fauna of my the Apus pool at God's Hill is highly remarkable consisting of five species of which four are rare or very rare in the British Isles: Chirocephalus diaphanus; Triops cancriformis, Macrothrix hirsuticornis f. arctica; and Alona elegans. The remaining species is Chydorus sphaericus, the commonest of all Cladocera, but rarely found in temporary pools.

Macrothrix tenuicornis.

Witt's Farm, ~~God's Hill~~ Godshill, Hants, 8.6.50., very abundant, eggs c.4 (0 to 8), temperature 24 C.

This species is often recorded as M. rosea but it is certainly not the same as Monoculus rosea Jurine. Scourfield and Harding (1941) call it Echinisca tenuicornis but it is now generally agreed that the genus Echinisca must be abandoned (Brehm, 1933.)

The species has often been confused with M. hirsuticornis, but there is no real difficulty in separating them. M. tenuicornis has slender antennules not broadening at the tip; it has two conspicuous lateral ridges on the head; and the anterior margin of the head bulges out in front of the eye; the abdominal setae are borne on a distinct conical process. In all these features it differs considerably from M. hirsuticornis.

This is a southern species and the British Isles are at the extreme northern edge of its range. It is very rare and in the last hundred years it has only been collected from some 8 widely separated localities, five of them in Ireland. The only English records are for a pond on Larling Heath, Norfolk (Gurney, 1933), and for Highlow Tarn, in the Lake District (Scourfield and Harding 1941). These are the only two occasions on which it has been recorded in the last 50 years. Scourfield and Harding give its habitat as ponds and ditches. This vague description fits my locality, and seems to be all that can safely be said. I, at least, cannot find any significant features common to a duck-pond, such as my Hampshire locality, and a high, peaty tarn, such as Highlow Tarn.

Lathonura rectirostris

Brothers Water, 17.8.49., scarce, eggs 2 to 8; Wray Boat Dock, Windermere, 8.8.49., very scarce, many eggs; Jesus Brook, x.3.48; Granta Inn Pool, 8.7.48., one only; Hampton Long Water, 27.1.49., numerous; Hjorte Söle 1, scarce above sphagnum and in outside puddles, eggs 4 to 7; Storre Gribsö, 3.8.50., IV, very numerous, eggs c.4; Log Sö, 5.8.50., IV, very scarce, eggs c.4.

Though this is not a common species it is probably less rare than is generally believed or than my records indicate. I have only found it w when I have included fragments of water plants in my collections, and it adheres to these very tenaciously. Jenkin (1928) has noted this behaviour under natural conditions. It is thus liable to be overlooked by collectors using ordinary methods.

As is well-known (Jenkin 1928), Scourfield and Harding 1941, etc.) this is not a bottom form, unlike most Macrothricidae. In general it occurs amongst thick vegetation in the same sort of habitats as *Simocephalus* spp.

Poulsen (1928) thinks that the species is confined to weakly alkaline waters, not occurring in acid waters. It certainly may occur in very acid waters and my records indicate that it is almost indifferent to the pH. of the habitat. Professor Berg tells me that he holds the same opinion.

The comparative rarity of this species is not easily explained. It is however possible that it needs comparatively stable environmental conditions. All my localities; large lakes; highly acid lakes; and semi-lenitic waters can be considered as being comparatively stable in this sense.

Drepanothrix dentata

Wharton Tarn, 14.8.49., numerous; Wray Mires II, 24.8.49., very numerous; Wiseen II, 24.8.49., very scarce; The Tarns, 27.8.49., II, very scarce.

According to Scourfield and Harding (1941) this rather rare species occurs amongst weeds at the margins of ponds and lakes. It is a species which always shows a strong negative phototropism, (Birge 1918) and so is usually found hidden under detritus. Berg (1928) has only found it in three localities, all woodland ponds. It occurred on miry bottom in half to two metres depth.

Despite the fact that it is a bottom species my records do not show any very marked association with different types of bottom, and Smyly (in litt.), informs me that its distribution in Three Dubs Tarn is not correlated with the nature of the bottom, but is correlated with the thickness of vegetation.

General records show the species is much more common the the northern portions of the British Isles, than it is in the southern portions. It appears to be extremely rare in the London area. My localities and most of those recorded in the Scourfield Ms. are for habitats that have soft water, but are not markedly dystrophic. The species appears to be restricted to somewhat acid waters. The evidence available is not sufficient to show whether or no this is due to inability of the species to withstand high calcium concentrations or to competition.

Streblocerus serricaudatus

Drunken Duck 1, 6.8.49., very scarce; 27.8.49., scarce; Yew Tree Tarn, 13.8.49., scarce; Tarn Hows, 13.8.49., III, very scarce; Hjorte Söle, 1, 29.7.50., very scarce, eggs 2, 25.8.50., scarce.

All authors accept this species as being almost completely confined to very acid localities, though Poulsen (1928) has collected individuals from a pond with pH. 7.6. It is normally considered to be a sphagnophile (Berg 1929, Pacaud 1939, Scourfield and Harding 1941), but it is noteworthy that comparatively few of the published observations refer to true bog pools, the species being normally reported from the margins of acid lakes and pools, often, but not invariably associated with *Sphagnum*. Three of my collections are for such localities and in none of them was there much sphagnum, though in all there was plenty of vegetation. The species is known from Windermere and Rydalwater, which are unlikely localities for a sphagnophile. It is more correct to say that this species is almost confined to strongly acid waters. Since it is a bottom form and is usually collected in shallow water, it will often be associated with *Sphagnum*, though the association is not essential. In structure and habits the species approaches very closely members of the genus *Macrothrix* and it seems not unlikely that it is competition with these which restricts it to acid waters, since Poulsen's record shows that it can live in slightly alkaline waters. Such occurrences are however very unusual, and Brehm (1933) cites this species and *Acantholeberis curvirostris* as two exceptions to his generalization that as a group the Cladocera are largely indifferent to the pH. of the medium.

Acantholeberis curvirostris

Loch a 'Phuirt-Ruaith, 7.9.48., very scarce; Loch Skiport Hill Pool, 9.9.48., very scarce; Rueval 1, 9.9.48., very scarce; Hjorte Söle 1, 29.7.50., abundant over Sphagnum, eggs c.4 (2 to 6); 25.8.50., plankton throw, one only; Hjorte Söle 2, abundant, eggs mostly 0 to 2; Bonderness Mose 2, 3.8.50., very numerous, eggs c.2; Bonderness Mose 3, 3.8.50., one only, = eggs; Madum Sö, 9.9.50., very numerous over 8 eggs.

This species is so strictly confined to strongly acid localities, that it may be taken as an indicator of high acidity with complete confidence. I have not been able to find a single record of this species from non-acid waters, and, as Poulsen (1928) says, it is normally only found in very acid waters, being uncommon in slightly acid waters. It is generally considered to be a sphagnophile, and is in fact characteristic of bog pools, as my records show. It may however occur away from spagnum in shallow waters around the margins of acid lakes. There is for instance no Sphagnum in either Loch a' Phuirt-Ruaith, or Madum Sö.

Acantholeberis curvirostris is not strictly a bottom form, judging by its behaviour in the laboratory. Though it often moves along the bottom it spends a large proportion of its time swimming freely. It is also much larger than most species of bottom-living Macrothricids, so that it is impossible to regard any of them as likely competitors. Thus the restriction of this species to acid waters is probably due to its inability to stand the conditions present in more alkaline localities, a feature which is most unexpected in a Crustacean. It may be that the real limiting factor in the distribution of this species is the necessity for very constant chemical conditions of the environment. Such constancy is shown to a high degree by very acid waters.

Eurycercus lamellatus

Upper Loch Altabruig, 31.8.49., one very young individual only; Loch a ' Phuirt-Ruaith, scarce, all small; West Loch Eilean a 'Ghille, 8.9.48., numerous, a few large; Loch Skiport Hill Pool, 9.9.48., very abundant many large; Loch Ness, 23.6.50.; Lower Greasborough Dam x.7.48., margins only, very scarce; Wray Boat Dock, Windermere 5.8.49., very numerous, eggs high, 8.8.49., abundant, 12.8.49., very abundant, 30.8.49., not very numerous, small; Wray Jetty, Windermere, 8.8.49., abundant, 12.8.49., very abundant, high eggs; 30.8.49., very abundant, large, high eggs; Wray Boat House, 30.8.49., not very numerous, high eggs; Low Wray Bay, 12.8.49., very scarce; Brathay Mouth, Windermere, very scarce, small; Blelham Ia, 18.8.49., very scarce, young only; Blelham Ib, 18.8.49., numerous; Blelham IIIb, 19.8.49., not very numerous, young only; Blelham IVb, very scarce, young only; Tarn Hows III, 13.8.49., not very numerous, eggs low, 27.8.49., numerous, mainly small; Brothers Water I, 17.8.49., scarce, mostly young; Coniston Water III, 20.8.49., numerous, all small; Easedale Tarn, I, 22.8.49., very scarce all small; Wray Mires II, scarce, mostly small; Wiseen II, 24.8.49., numerous, large, few eggs; Drunken Duck Tarn, 27.8.49., very scarce away from reeds, very numerous in thick 'reed' bed large, many eggs; Diana Pond, Bushy Park, 12.1.49., numerous, very pale; Hampton Longwater, 27.1.49., numerous, 26.2.49., numerous; Hampton Wick Pool, 3.2.49., under ice, scarce; Little Stanmore 1, numerous in Potamogeton; Little Stanmore 2, 9.7.49., in Potamogeton, not very numerous, eggs low, 12.10.49., not very numerous in thin weeds, scarce in thick weeds, eggs very low, 1 to 3; Cam above St. John's, Cambridge, 8.7.48., two; John's - Trinity Dyke, 8.7.48., moderately abundant, 26.7.48., abundant; Granta Inn Pool, 8.7.48., two, 10.8.48. adults scarce, young numerous; Jesus Brook, 18.7.48., scarce: Coldham Brook, 25.7.48., one only; Dyke 448.578., Cambridge, 4.8.48., abundant; Dyke 448 576, Cambridge 10.8.48., numerous; Fowlmere, Thetford, 10.7.48., numerous; Badstue Dam, 20.7.50., very numerous, many eggs, 30.8.50., scarce, only one adult; Storre Gribsö, III, one young only; Esrum Sö, Sorup Bay, 15.8.50., numerous, large, eggs c.12: Karlssö 19.8.50., very scarce, one with 8 eggs; Borressö, 10.9.50., very abundant, not in reeds.

All authors are agreed that this species is characteristic of the weed-zone of lakes and large ponds, and scarcer in small ponds. Poulsen (1928) also records it in small ponds without vegetation, but this is an unusual situation. Poulsen gives not details as to other characters of these ponds which might throw light on the occurrence. My only records from very small localities are for those such as Jesus Brook, which are semi-lenitic, or those such as the Loch Skiport Hill,Pool which are acid and peaty.

This species is the most nearly adapted to life in lotic environments of all species of Cladocera. It is recorded from a very large number of slowly flowing rivers, where, as in the Cam, it occurs amongst the marginal vegetation. There are a few records for rather fast rivers (e.g. Erichsen Jones 1949, Frost 1950). In such situations it may occur on the bare bottom of small pools in the main stream.

Poulsen (1928) considers that the species is characteristic of weakly acid or alkaline waters, and comparatively rare instrongly acid or strongly alkaline waters. My records show no such preference, and it seems certain that the species is really indifferent to a very wide pH. range.

E. lamellatus is clearly very catholic in its habitat preferences, and the rarity with which it is found in small ponds, which appear to be perfectly suitable, is thus rather surprising. Pacaud (1939) suggests that it is very sensitive to pollution. This is probably true, but cannot explain all the facts, since the species is definitely uncommon in unpolluted small ponds. For this, as for other species showing a similar distribution I believe that stability of environmental conditions is an important factor.

The Chydorinae:

In most of the species of this sub-family distribution is controlled chiefly by the conditions of the micro-habitats present in lakes and ponds. Thus it is not usually possible to associate species with any particular type of water body, and quite often there is not correlation with the larger zones within a locality. In these circumstances only complete lists of all field records would be useful. For this reason I shall not give locality lists in detail except for a few species of special interest, and for rare species.

Camptocercus rectirostris

Esrum Sö, 25.7.50., Pipervang IV, very scarce, 2 eggs; Storre Gribsö 3.8.50., II, very numerous, IV, abundant.

This species is said to be common in Denmark (Berg 1928), but it is rare in the British Isles (Scourfield and Harding 1941). My two records do not allow me to add to knowledge of its occurrence, but they agree with the distribution given by Berg, 'who considers it typical of the margins of lakes and large ponds when there is some vegetation. In both localities the species was living in fairly exposed situations where the weeds were thin. These situations approached those in which Alonpsis elongata is found in the northern lakes of the British Isles. The two species are very similar in build and behaviour, though Alonopsis elongata is more of a bottom form. This latter species is very rare in Denmark and it seems possible that the distribution of the two species is partly determined by competition. It is noteworthy that Pacaud also considers that situations where there is a fair amount of water-movement are most favourable to this species.

Poulsen (1928) makes the rather surprising statement that the species is characteristic of acid waters. Its occurrence in Esrum Sö, and in other highly calcareous Danish Lakes (Berg 1929) is sufficient to disprove such a statement, as is rarity in northern English Lakes.

Camptocerecus Lilljeborgii

Teylgaard Sö, 22.7.50., outer edge of reed-beds, scarce, eggs 1; Log Sö, 5.8.50., I, scarce, IV, very numerous; Karlssö, 19.8.50., scarce; Valve of Health Pond, Hampstead Heath, 21.10.50., 2 males only.

This species has similar general habitat requirements to the last, but is definitely rarer (Berg, 1929, Scourfield and Harding, 1941).

Berg characterises this as occurring in fairly large pools and near lake shores, whilst for C. rectirostris he gives large pools and lake shores. The implied distinction is that C. lilljeborgii is usually found in somewhat smaller habitats than those characteristic of C. rectirostris. This is borne out by his records. My records are also all for habitats of medium size. Thus size of habitat probably influences which species of Camptocercus is present.

The record for the Vale of Health Pond, if established by the discovery of females will considerably extend the known range of this species in the British Isles. I think that my identification of the males was probably correct, since the two British species appear to differ considerably according to Lilljeborg's figures, but obviously records of importance cannot be based on males alone. The only recorded English localities are in Norfolk.

Alonopsis elongata

Loch Druidibeg, 3.9.48., I, very scarce; Loch Druidibeg II, 9.9.48., very scarce; Loch Druidibeg III, 9.9.48., scarce; Loch a Machair, 4.9.48., very scarce; Loch a 'Phuirt-Ruaith, 3.9.48., numerous; West Loch Eilean a 'Ghille, 7.9.48., very numerous away from weeds; Loch Teanga, 9.9.48., numerous; Loch Skiport Hill Pool, 9.9.48., numerous; Malham Tarn x.3.48., not very numerous; Red Tarn, Helvellyn, 4.8.49., not very numerous; Blelham Ic, 4.8.49., not very numerous, Blelham Ia, 18.8.49., abundant; Blelham Ib, 18.8.49., scarce; Blelham IIIb, 19.8.49., not very numerous; Blelham Iva, 19.8.49., numerous; Low Wood, Windermere, 10.8.49., very scarce; High Wray Bay, 16.8.49., scarce; High Wray Bay, Boat Slip, 16.8.49., scarce; Low Wray Jetty, 30.8.49., very scarce; Wastwater, 10.8.49., abundant; Ennerdale, 10.8.49., very scarce; Tarn Hows I, 13.8.49., scarce; Tarn Hows II, 13.8.49., very abundant, 27.8.49., very numerous; Tarn Hows III, 13.8.49, very numerous; 27.8.49., numerous; Coniston Water II, 13.8.49., extremely scarce; 20.8.49., III, very numerous; Ullswater I, 17.8.49., numerous; Ullswater II, 17.8.49., scarce; Ullswater III, 17.8.49., scarce; Brothers Water I, 17.8.49., very scarce; Brothers Water II, abundant; Codale Tarn, 16.8.49., abundant, 15.10.49., numerous; Grizedale Tarn, 22.8.49., a few fragments (the only trace found of any Cladocera after over half an hour's collecting); Easedale Tarn, I, 22.8.49., very numerous; Easedale Tarn, II, 22.8.49., numerous; Easdale Tarn, 15.10.49., numerous, males; Rydal Water 30.8.49., in plankton, scarce; Loch Ness 23.6.50.; Bure Sö, 11.8.50., II, abundant.

This is probably the most frequent of all Cladocera in the lakes of the mountain area of the British Isles, but is unknown from the Midlands, and S. and E. England (Scourfield and Harding 1941). It is extremely rare in Denmark (Berg 1929). It is known from the Faeroes and the Swedish Highlands, but not from Iceland or the true arctic (Poulsen 1939). It is unlikely that temperature is the factor causing this apparently northern distribution. I have found it often in localities with water temperature in the region of 20°C, and once in water at 23.5°C (Tarn Hows 27.8.49.). Thus there is no reason why the species should not occur in the S. and E. of England, at least in spring and autumn. Other features must be responsible for its distribution.

Alonopsis elongata is dominantly a species of large lakes, and high tarns, in the more barren of which it may be the only cladoceran present in any numbers. It is typically found in somewhat exposed or very exposed situations, where again it may be the only cladoceran present. It is much less frequent and usually less abundant in sheltered situations. It may occur in thin vegetation and even in thin reed-beds, but is rare in thicker vegetation. It is normally found on rather coarse gravelly or rocky bottoms, more rarely on sand, very rarely on silt. The nature of the bottom and the degree of exposure seem to be the two most important factors and their actions are to some extent independent.

These habitat requirements go a long way towards explaining the absence of the species from S. and E. England, since there must be very few localitites in which they are met. They do not, however explain why *A. elongata* is absent from most of the large Danish Lakes, such as Esrum Sö (Investigation of this lake, Berg 1938, has been so thorough that we can be certain that the species, if not absent, is at least extremely rare.)

It is clear that hardness of the water does not provide a satisfactory explanation of the distribution of this species. Whilst most of the large lakes and tarns in the north of England have soft to very soft water a few such as Malham Tarn, have very hard water. *A. elongata* appears to be flourishing at Malham (though I have recorded it as not very numerous, it was easily the most abundant animal in the rather sparse littoral fauna of the stony shores of this lake.)

A more plausible suggestion is that it is prevented from becoming established in the large Danish Lakes by competition with *Camptocercus rectirostris*, the latter species being favoured by the more abundant food-supply in these eutrophic lakes. If this were so one would expect the Danish localities for *Alonopsis elongata* to be less eutrophic than most Danish lakes. This is probably true of 4 of Berg's localities. The fifth however is according to Professor Berg very highly eutrophic and polluted (Soro Sö). I have not seen this lake myself so I do not know whether it has any peculiar features which would offset its eutrophy. This explanation of the rarity of *A. elongata* in Denmark is thus not entirely satisfactory, whilst no alternative simple explanation seems to be tenable, so that the answer to this question must be left undecided.

Alonopsis ambigua

Sorte Dam Strödam, 25.8.50., one only; Vilde Ande Dam, Strödam, 25.8.50., very numerous.

Virtually nothing is known of the ecology of this extremely rare and sporadic species. In England it is only known from one pool in Norfolk (Gurney 1905), whilst in Denmark the only record prior to mine was that of Berg (1929) for the Sorte Dam, Strödam). The species appears to be a regular inhabitant of this pool, whilst in most of its other recorded localities it has only been found once. Its discovery in another very comparable pool on the same estate enables me to give some tentative theories as to its ecology. Both of these pools are very shallow pools largely covered with Lemna. Their bottom deposits consist of a thick layer of decaying vegetable matter, mainly Lemna and Lemna mud. I found the species only in and about these deposits. Thus it can be tentatively assigned to the same ecological group of species as Ceriodaphnia setosa.

Acroperus harpae
including A. angustatus

I have records of this species from 2 lakes in S. Uist; from 4 localities in Cambridge; from Fowlmere, Thetford; from a pool near Loch Ness; from Lower Greasborough Dam, S. Yorkshire; from 3 lakes and 2 tarns in the Lake District; from 7 localities in London; from 6 lakes and 4 pools in Zealand; and from 1 lake in Jutland.

A. angustatus is sometimes recognized as a distinct species (Scourfield and Harding, 1941), sometimes treated as a form of A. harpae (Berg, 1929). The latter treatment seems to me most correct. I have found a number of populations, such as that in Hjorte Söle, Denmark, which contained typical individuals of both 'species' and every possible intermediate. Many, probably the majority of populations which I have seen, consist of individuals more or less intermediate between the two species, though forms approaching typical *A. harpae* are the most common.

This species is well-known as a typical weed-inhabiting form, commonest in the littoral region of large localities; but sometimes occurring in smaller waters (Berg, 1929; etc.) Poulsen (1928) finds that it is indifferent to pH.

My collections agree with these conclusions, but I am able to amplify them. In morphology and behaviour *A. harpae* closely approaches *Alonopsis elongata*, and the species of *Camptocercus*. It is less of a bottom form than *Alonopsis* and somewhat smaller than *Camptocercus*, but it probably competes to some extent with each of these species, and its distribution is somewhat complementary to theirs. I have found *Acroperus harpae* with both *Alonopsis elongata*, and *Camptocercus spp.*, and Pacaud also finds that *Acroperus* and *Camptocercus* are commonly associated. The detailed distributions of the species differ, however. *Acroperus* is most abundant in thick vegetation, and is rarely found in exposed places, even where the vegetation is comparatively dense. On the other hand *Alonopsis* and *Camptocercus* are rarely abundant in thick vegetation, though often abundant in thin marginal vegetation. They are usually most abundant in somewhat exposed situations. The interactions between these species are rather complex, and are further complicated by relations with *Pleuroxus truncatus*, which frequents somewhat similar habitats (see below.)

Graptoleberis testudinaria

Granta Inn Pool, 8.7.48., one; Jesus Brook, x.5.48., numerous; Chalk Lane Pool, 23.5.49., scarce; Hjorte Söle 1, 29.7.50., marginal puddles, scarce; Storre Gribsö, 3.8.50., IV, not very numerous; Lille Fonstrup Dam, 14.8.50., scarce; Fönstrup Dam, 14.8.50., very scarce; Karlssö, 19.8.50., scarce; Vilde Ande Dam, Strodam, 25.8.50., very numerous; Praestevang 1, 2.9.50., one only, empty.

This species is almost certainly more common than my records indicate. Its minute size and burrowing habits make it very difficult to find in collections. These habits probably also account for the well-known fact that it is very unusual to find more than a few individuals of this species in any collection.

Most authors, e.g. Scourfield and Harding (1941), regard this as a bottom form occurring dominantly amongst weeds. Poulsen (1928), however notes it as occurring on muddy bottoms without showing any marked association with the presence of vegetation. My results support this conclusion. Most of the habitats from which I have collected the species are weedy, but it is distributed within, without regard to the weed-cover, on a bottom of silt or mud. I have not found it however in the typical brown lake muds frequented by Ilyocryptus sordiddus and Leydigia. Restriction to a particular type of mud seems to be the dominant feature of the ecology of this species. Since the required type of mud, normally occurs in association with vegetation, a spurious correlation is produced between the occurence of this species and the vegetation of the locality.

Poulsen (1928) regards this species as acidophil, and as rarely occurring in markedly alkaline waters. My results do not support this conclusion, but indicate that the species is indifferent to pH.

Leydigia leydigi

Cam above St. John's, 8.7.48., one only; Hobson's Brook, Cambridge, 17.7.48., one only; West Ditch, Coldham Common, 25.7.48., scarce; Coldham Brook 25.7.48., very scarce; Dyke 448.578., Cambridge, 4.8.48., very scarce; Lower Greasborough Dam, 17.9.48., scarce; Hampton Wick, 12.1.49., scarce, 32.49., under ice, very scarce; Golder's Green 1, 7.6.49., scarce; Warren Pond, 22.10.49., very scarce; Connaught Water, 25.3.50., very numerous; Hampstead 3, 27.5.50., in rushes scarce; Hampstead 1, 27.5.50., scarce; Island Pond, Queen Mary's Garden, 8.5.50., very scarce, 25.10.50., very scarce; Water Lily Pond, Queen Mary's Garden, probably throughout the year, though I have no records for November to February; Children's Boating Lake, Regent's Park, throughout the Autumn and Winter, not in summer, ephippial reproduction occurs in autumn; Regent's Park Lake, throughout autumn, winter and spring, rarely in summer, ephippial reproduction in autumn and late spring.

According to Scourfield and Harding (1941) this species is common and widely distributed in the British Isles. In Sweden it is sporadic (Lilljeborg 1900), whilst Berg has only found it in four localities, all lakes, in Denmark. It does not occur in Iceland or the arctic (Poulsen 1939). Temperature cannot be the factor limiting the northwards spread of this species, since it is often abundant in winter. In my experience it can live and reproduce under ice, and Berg (1929) has found it flourishing under ice in Denmark.

The typical localities for this species in England are small waters according to Scourfield and Harding, and this agrees with my experience. However, this apparent preference for small bodies of water is probably spurious as in the case of *Ilyocryptus sordidus*, which has a very similar habitat requirements.

Leydigia leydigi is in my experience almost confined to typical brown lake muds, or the very similar deposits in lenitic environments, and normally remains burrowing in them. In shallow waters, as the Children's Boating Lake, it may, when very abundant, sometimes become partially planktonic. However this behaviour does not appear to be correlated with any special environmental conditions. This species, as *Ilyocryptus sordidus*, occurs in Frederiksborg Slottssö, and in Karlssö, though I failed to find it there. It is probably present in all lakes with suitable deposits of mud.

This species is distinguished from the closely allied *Leydigia macrodonta* G.O. Sars by : 1, the non-triangular ocellus; 2, the presence of very faint reticulations in the posterior region of the carapace; 3, the possession of a definite not vestigial spine of the claw; 4, the shorter lateral spines an the post-abdomen; and 5, there being two long spines in each group lateral spine group.

Jenkin (1934), described, a form, *Leydigia macrodonta v. louisi* which she herself pointed out approached *L. leydigi* very closely. The carapace markings and spination of the post-abdomen are as in *L. Leydigi*, but the spines are noticeably long and slender (in her figure the longest spine is 58% of the claw length), and the ocellus is triangular. The claws have a definite basal spine.

The form in Regent's Park Lake, which is certainly *L. leydigi*, closely resembles this variety of Jenkin. The spinulation of the post-abdoman is almost identical, but the longest spines are not quite so long. (modal length of 10 individuals 46% of the length of the claw.) The basal spine is very variable. It may be as large as in typical L.leydigi, or even smaller than in Sars figures of L.macrodonta. The carapace markings are exactly as those described by Jenkin. The ocellus is as in typical L.leydigi.

According to Lilljeborg's figures the spines of typical L.leydigi attain to 40% of the length of the claws, whilst from Sars' (1916) figure of L. macrodonta they reach 63% of the length of the claw in this species.

Thus there are a continuous series of forms leading from L.leydigi to L.macrodonta, and they must be regarded as forming one species. Tentatively, I recognize three geographic subspecies: Leydigia leydigi leydigi, holarctic and N.Africa; Leydigia leydigi louisis, E.Africa; and Leydigia leydigi macrodonta, S. Africa.

Leydigia acanthocercoides

Children's Boating Lake, Regent's Park, 11.10.49., abundant, many young, some ephippiate, males, 4.11.49., numerous, males, 18.11.49., numerous, mostly empty, 30.10.50., very scarce, ephippiate; Regent's Park Lake, July to November, ephippial reproduction in October after which the species becomes very scarce.

This is a rare species confined in the British Isles to the S. and E. of England, and to Ireland (Scourfield and Harding, 1941).

In my localities it appears to replace L.leydigi in the summer. It certainly does not winter. Temperature thus seems to be an important factor in its distribution. Apart from this I can detect no way in which its requirements differ from those of L.leydigi.

Oxyurella tenuicaudis

Praestevang 1, 22.7.50., scarce, 1.8.50., very scarce. This is the same as Alona tenuicaudis. Nothing definite is known of the ecology of this rare species. Its occurence, burrowed in Lemna, mud at Praestevang 1, suggests that it may belong to the Ceriodaphnia setosa ecological group, but there is certainly not enough evidence available to prove this.

Alona affnis

I have records of this species from the Loch Skiport Hill Pool in S.Uist; from Loch Ness; from Blelham, Ullswater, two tarns and the Drunken Duck Pool in the Lake District; from the Middle Revenfield Dam in S. Yorkshire; from Groby Pool, Leicester; from 18 localities in Cambridge; from 6 localities in Zealand; and from 1 lake in Jutland. I have found specimens in every month of the year. With a single exception all my records are from bottom collections. This exception is its occurrence in considerable numbers in the plankton of Queen Mary's Reservoir, on 6.2.51.

Scourfield and Harding (1941) say that this species is very common and occurs among weeds by the margins of ponds and lakes. Poulsen (1928) says it is commoner amongst weeds, but also occurs in weed free areas.

My records show that there is no particular association between this species and littoral vegetation. It is commonly present amongst weeds, but is often found away from them. It is equally abundant in adjoining weed-free and weedy areas, provided that the bottom conditions and the degree of exposure are similar.

Though odd individuals may occur on a wide variety of bottoms, I find that this is predominantly a species of sandy bottoms, becoming very rare on muddy bottoms. Unlike Macrothrix laticornis it is not restricted to consolidated sands but may occur on the extensive areas of loose sand found in large lakes. In such stations at Ullswater and Esrum Sø, it was fairly numerous, and almost the only cladoceran present.

It can tolerate moderate degrees of exposure but is not found in very exposed situations, and is more common in sheltered places, provided that the other habitat conditions are satisfactory. In my experience the species is indifferent to pH. and to the size of the habitat.

Alona quadrangularis

I have records of this species from two lakes in S.Uist; from the Lower Greasborough Dam, in S.Yorkshire; from 12 localities, including Regent's Park Lake in London; and from the Arressö in Denmark.

Scourfield and Harding (1941) say that this species occurs in more or less acid waters, whilst Scourfield (1895) thinks that it tends to replace A.affinis in the soft-water lakes of N.Wales. Poulsen (1928) also considers that it is most characteristic of acid or slightly acid waters. Berg (1929) records it from a number of lakes with hard water.

My experience agrees with that of Berg, and I am not at all convinced that either of these two species is affected by pH. to any significant extent. I can detect no reliable differences in ecology between A.affinis and A.quadrangularis which often occur together. Berg has expressed the opinion that the two are not really distict species, and I also feel doubtful about their distinction. Certainly there are forms that disagree with both species but clearly belong to this complex. Brehm (1933-), makes no attempt to distinguish the various members of the affnis group, and until such a revision is carried out it is unsafe to attempt to distinguish differences in ecology.

Alona rectangula

Jesus Brook x.5.48.; Highgate 2,13.5.50., numerous arround algae detritus masses; Children's Boating Lake, 12.10.50., very scarce, carapaces had been found in two previous collections: Karlassö 19.8.50., very scarce;

Praestevang 1, 2.9.50. one young.

Scourfield and Harding (1941) only say of this species that it is common in weakly acid or alkaline waters. Poulsen (1928) considers that it occurs most often in shallow vegetation rich water. My rather miscellaneous collections agree with these opinions but do not enable me to add anything to them.

Alona costata

Log Sø, 5.8.50., III, very scarce; Esrum Sø, 15.8.50., Sorup Bay, scarce; Praestevang 1, 2.9.50., very scarce.

My failure to find this species in the British Isles is rather surprising, since it is supposed to be common (Scourfield and Harding 1941). Poulsen (1928) considers that it is the commonest *Alona* in the vegetation zone of lakes and large ponds. My specimens are from such habitats with plentiful vegetation, but even in Denmark they indicate the species to be rare rather than common. It is well known that personal idiosyncrasies of collecting method may cause a worker to overlook a species, that other workers find fairly common. Even making due allowance for this possibility I still feel that, had this species been as common during the last three years as previously, I would have found it more often. There is at least a *prima facie* case for a drastic reduction in numbers.

Alona elegans

Apus Pool, ~~God's Hill~~ Godshill, 19.3.50., numerous.

Virtually nothing is known of the ecology of this extremely rare species which has only been found in a very few localities in S.Germany, England, and North Africa (Brehm 1933), though it has been known for over 80 years. The only English records are for small pools in E.Yorkshire and Norfolk (Scourfield and Harding 1941, Scourfield, 1903). All that can safely be said from these facts is that it is a species of small habitats. Presumably it cannot stand highly polluted waters, since it has never been recorded from *Daphnia* ponds.

Rhynchotalona falcate

Storre Gribsø, 3.8.50, III, abundant.

This is a burrowing form (Wesenberg-Lund 1939 , etc.) but does not frequent muddy habitats. Poulsen (1928) only found it in a few localities, which all had pH values between 7.1 and 7.9. This would indicate that the species prefers weakly alkaline waters. Its abundance in the strongly acid Storre Gribsö is against this, as is also the fact that it is commoner in the north than in the South of England (Scourfield and Harding, 1941).

Rhynchalonella nov.gen.

Lynceus rostratus Koch has been very variously placed in the past. By Lillijeborg (1900) it is included in *Lynceus* (= *Alona*). Birge (1918) places it in *Alonella* s.n. Brehm (1933) also treats it as a species of *Alonella*, though in his list of African Cladocera (1933b) he records it as *Leptorhynchus* (= *Rhynchotalona*). Most recent authors, such as Pulsen (1928), Berg (1929) and Scourfield and Harding (1941) treat it as a species of *Rhynachotalona.* Birge first recorded this species for N. America as a species of *Pleuroxus* (*Pleuroxus acutirostris*).

It is clear that its exact relationships are uncertain, and it has no particular affinity with any of these genera. For this reason I am proposing a new genus to include it.

The characters of Rhynchalonella are as follows:- Moderately compressed, somewhat elongate low forms, with a general build somewhat recalling that of a Pleuroxus of the striatus group. Dorsum only slightly arched, not crested. Free hind margin of carapace more or less perpendicular to the dorsal and ventral margins and less than half the greatest height of the carapace. Carapace longitudinally striate in the type species; reticulate in Rhynchalonella dentifera. Rostrum long, slender, recurved, and acutely pointed. Ocellus almost, or quite as large as the eye. The post-abdomen is of moderate size and aloniform. The pre-anal angle is not well-marked. The distal portion of the post-abdomen is rounded. There are a number of short marginal denticles but no lateral fascicles. The anal emargination is not very deep. The claws are of moderate length with a single basal spine. The males closely resemble the females, but the post-abdomen is somewhat tapering.

Type species; Lynceus rostratus Koch = Pleuroxus acutirostris Birge
= Rhynchalonella rostrata (Koch)

Other species: Leptorphynchus dentifer Daday = Alonella dadayi Birge
= Rhynchalonella dentifera (Dayday)

The genus is distinguished from all species of Alona by the very much longer rostrum and by the short free posterior carapace margin. From Pleuroxus it is distinguished by the larger ocallus, the presence of one, instead of two, basal spines on the claw, and the different structure of the post-abdomen.

From Rhynchotalona it is distinguished by the short free hind-margin of the carapace, the rounded as opposed to angular post-abdomen, the absence of lateral fascicles, and the shorter rostrum which is not flattened and bifid in the male.

From Paralonella (perhaps best treated as a sub-genus of Alona) it is distinguished by the long rostrum, the more elongate form, and the absence of lateral fascicles on the post-abdomen. From Pleuroxalonella (sub-genus of Alonella)- it is separated by the more elongate form, the longer rostrum, and the presence of only one instead of two basal spines. From Alonella s.s. it is readily distinguished by the aloniform rather than chydoriform build; the aloniform rather than chydoriform shape of the post-abdomen, the longer rostrum, and the different type of carapace markings.

Rhynchalonella rostrata

I have records of this species, usually in small numbers from Hampstead 1, Hampstead 2, Highgate 2, the Vale of Health Pond, Hadley Wood Lake, and the Eagle Pond in London; and from the Teylgaard Sö, Log Sö, and Estrum Sö, off Pipervang in Zealand.

This species has been considered in the past to prefer sandy bottoms but Berg (1929) disagrees with this opinion as he claims to have found it on miry bottoms. Whilst two of my records (those for the Teylgaard Sö and the Log Sö are for more or less silty bottoms which could not be classed as sandy, all the others are for definitely sandy bottoms. Thus the species does in fact occur far more commonly on sandy bottoms than elsewhere. The record for the Esrum Sö was from loose sand where a few of the present species were associated with the far more num~~b~~erous Alona affinis.

Pleuroxus truncatus

This is one of the commonest Cladocera. I have records for 4 lakes and 2 pools in S.Uist; for 3 pools in S.Yorkshire, for Loch Ness and a neighbouring pool; for 9 lakes, 4 tarns, 3 pools and a slow stream in the Lake District; for Fowlmere and Fowlmere Pool, Thetford; for 5 localities in Cambridge; for 5 localities in London; for 5 lakes and 10 pools in Zealand; and for 3 lakes in Jutland.

The species seems to be indifferent to pH., my localities ranging from the very acid Hjorte Søle to the highly alkaline hard-water Jaegerbakke Dam.

The species is almost always said to be a characteristic form of thick vegetation (e.g. Poulsen 1928, Scourfield and Harding 1941); but in my experience it is by no means confined to such habitats, though they are admittedly the most usual. In small ponds P.truncata commonly becomes planktonic, as at Old Denaby Pool, S.Yorkshire, whilst in some of the larger lakes it may be a true bottom form occuring away from vegetation. In such habitats it competes with Alonopsis elongata and it may largely replace this species, even on exposed stony shores, if there are plenty of algae present. This was the situation when I collected at Ennerdale Water.

In small pools where it may be the only chydorid present, apart from Chydorus sphaericus it seems to be largely independent of the nature of the bottom; but in larger waters it is rarely found over muddy or even very silty bottoms. Smyly informs me that the species is most frequent away from mud in Three Dubs Tarn. (Lake District)

Pleuroxus aduncus

I have records of this species from the two Greasborough Dams and one pool in S.Yorkshire; from Groby Pool, Leicester; from two localities in Cambridge; from 5 pool and a sandy bay of Regent's Park Lake in London; from Praestevang 1, and the river Pole in Zealand; and from Borressö in Jutland.

Scourfield and Harding say that this species occurs in mud and amongst weeds. Poulsen (1928) says it occurs in thick vegetation. Neither opinion corresponds exactly with my experience. The species is commonly but not necessarily associated with vegetation, though usually only with sparse vegetation. It may occur on silty bottoms but is most usual on bottoms in which consolidated sand is the principal constituent, though usually only where a slight amount of silt is present. The habitat is thus intermediate in many respects between those of P.truncatus, and P.uncinatus. I have only rarely found it associated with these two species.

Pleuroxus trigonellus

My earlier records of this species are mostly unreliable since I confused it with P.aduncus I have difinite records from Tarn Haows; the Viaduct Pond, Hampstead Heath; Log Sö; Esrum Sö, Karlssö; Teylgaard Sö; and Ugl Sö.

These records do not allow me to differentiate clearly between the preferred habitats of this species and those of P.uncinatus. My impression is that it is intermediate in requirements between P.aduncus and P.uncinatus but much more extensive collections would be needed before

I should consider this to be established.

Poulsen (1928) regards this species as confined to alkaline waters, but my records show that this is not so. Both the Tarn Hows and the Ugl Sö habitats are slightly acid.

Pleuroxus uncinatus

I have rocords of this species from two pools in S.Yorkshire; from the river Cam; and 8 other localities at Cambridge; for 13 localities in London; and for 5 localities in Zealand.

This species is generally accepted as being a burrowing form occuring amongst mud and weeds in alkaline waters. If mud be taken to mean silt, rather than true lake mud my records agree very well with this statement. I have on rather numerous occasions obtained a few individuals on mainly sandy bottoms, but in all these cases there were more silty pockets, and these were no doubt the tru habitat of the *Pleuroxus.*

Alonella nana

Codale Tarn, 16.8.49., very scarce; Drunken Duck Pool, 27.8.49., scarce; Karlssö, 19.8.50., very numerous; Hjorte Söle 1, fresh carapaces in plankton haul; Teylgaard Sö, 2.9.50., probably numerous, in clear water.

There is little reliable published information on this species, though it is not uncommon. Poulsen (1928) regards it as being independent of vegetation which agrees with my experience. He considers that it is most often found in nearly neutral waters. My records on the contrary indicate that it is largely independent of pH.

The species is certainly much more common than records indicate, since it is almost inevitably overlooked unless found by accident, owing to its minute size (it is, just, but only just, visible to the naked eye), and cryptic behaviour. My records certainly only represent a fraction of the collections in which it must have occurred, and the same is almost certainly true of the records of many other workers. In these circumstances an attempt to define strictly its habitat requirements would be unscientific.

Alonella excisa

Peat pool, Mointeach Mhor, 31.8.48., very numerous; Pool near Loch Ness, 20.6.50., 27.6.50.; Codale Tarn 16.8.49, scarce; Blelham Tarn, Ib, 18.8.49., numerous, Blelham IVb, 19.8.49., numerous; Thirlmere, in plankton, 24.8.49., scarce; Hampstead 3, 12.11.49., amongst out weeds, very scarce; Storre Gribsö, 3.8.50., I, very abundant, III, scarce, IV, very numerous, Ager Sö 5.8.50., I, scarce, II, very scarce; Flats Pool, Hilleröd, 9.8.50., scarce; Bastrup Sö 11.8.50 in thick reeds very scarce.

This species is normally found amongst weeds, though it may also occasionally occur on the bottom away from vegetation (Poulsen, 1928), (Scourfield and Harding 1941).

Poulsen considers it to be an acidophilous species, and to occur only rarely in slightly alkaline waters, never in strongly alkaline waters. My records support this theory. They also indicate that it is a pronounced bryophile, though not confined to places where mosses are growing. Away from mosses I have mainly found it on detritus rich bottoms. It is really a bottom species, and its apparent association with vegetation may be the result of these bottom requirements.

Alonella exigua

Tarn Hows, 27.7.49, III, very scarce; Wray Boat Dock, Windermere, 30.8.49., very scarce; Log Sö, 5.8.50., II very scarce; Fönstrup Dam, 14.8.50., numerous.

Save for its greater rarity, which is agreed on by all authors, I can find no reliable differences in ecology between this species and the last. This is in agreement with the findings of other workers. Poulsen for instance gives almost exactly the same habitats for the two species.

As my records show I have never found the two together, and perusal of the Scourfield Ms, shows that collections with both species are very unusual. This is in agreement with the theory that they have a very similar ecology. Presumably they are prevented from occuring together by competition.

Pleuroxus Laevis

I have collected this species in: Blelham Tarn; Storre Gribsö; Log Sö; the Flats Pool, Hillerōd; Karlssö; Badstuedam: and Teylgaard Sö.

My limited data suggests that this species is mainly a form of silty to detritus covered bottoms.

Chydorus globosus.

Loch Altabruig, 31.8.49., abundant, West Loch Eilean a ' Ghille, 8.9.49, very scarce in weeds; Wiseen, 24.8.49., II, very scarce; Tarn Hows, III, scarce; Lower Brathey 7, I, scarce; Windermere, 30.8.49., Wray Boat Dock, scarce, Wray Jetty, scarce. Hampstead 2, 9.3.50., one only; Island Pond, Wanstead, 16.6.50., very scarce; Highgate 2, 5.7.50., in flags, very scarce; Log Sö, 5.8.50., III, very scarce.

My records are almost always for weedy habitats, and thus agree with the opinions of other authors (Berg, 1929, Scourfield and Harding 1941).

The species seems to be largely indifferent to pH.

Chydorus Sphaericus

This is the most abundant and widespread of all Cladocera but is not ubiquitous. I have records for 11 localities in S.Uist; for 20 localities in the lake district; for 26 localities in S.Yorkshir; for Loch Ness and a neighbouring pool; for Groby Pool. Leicester; for the River Avon, Hampshire; for 43 localities in the London area; for 6 localities in Cambridge; for 3 localities in Thetford; and for 22 localities in Zealand.

The first impression of this species is that it is virtually ubiquitous. It occurs in the plakton of lakes, and in tiny pools on high moors. It may be on any sort of bottom and amongst almost any sort of vegetation. It occurs at all seasons of the year. Perhaps for these reasons few workers have attempted to investigate the conditions under which it occurs. One of the few good investigations is that of Pacaud (1939). Pacaud concludes, that it is rare in small stagnant ponds, choked with vegetation, and that it is not able to stand a high degree of pollution unless the locality is very shallow. He concludes that low oxygen tensions are markedly unfavourable to this species and he also showed that it was not very resistant to low oxygen by experiments.

I also have found that this species is less common in weed-choked pools and in highly polluted habitats than it is elsewhere, but there are limitations to its distribution. It is very rare in temporary pools. I have only found it in 5 of these, four of which were of very unusual character. Though many such pools are often highly polluted, such pollution is not frequent enough in itself to explain the rarity of Chydorus sphaericus. It cannot be explained by inability to survive drought, since it can occur in these unusual temporary habitats. It would appear that the generally unfavourable conditions that develop in such pools, immediately before they dry up prevents *C.sphaericus* from becoming established.

Another rather striking limitation is the association of this species with filamentous algae, commented on previously by Berg (1929) *C.sphaericus* is almost invariably present and abundant in a locality in the immediate vicinity of filamentous algae, though it may be extremely scarce in other portions of the habitat. This is stikingly shown in Regent's Park Lake, where, except on the rare occasions when the plankton contains algal filaments, *C.sphaericus* is almost completely confined to the narrow fringing zone of *Cladophora*, andmay be unobtainable a few inches away from this. My observations also lead me to believe that this species only occurs in the plankton when this contains filamentous Diatoms or coarse filamentous myxophycean or *Tribonema* sp., though as I have not been very much concerned with the plankton the conclusion is only tentative.

Chydorus ovalis.

Ennerdale Fen 2.4.48., abundant; Stilligary Ditch, 3.9.49., very abundant, West Loch Eilean a ' Ghille 8.9.48., very scarce; Rueval B, 9.9.48, very scarce; Pool in Borran's Field, 6.8.49., abundant, 11.8.49., abundnat; Borran's II, Windermere, 6.8.49., very scarce, 11.8.49., not very numerous; Hjorte Søle, 29.7.50., foothole in bog, abundant.

This species has very much more sharply defined habitat requirements than the closely related *C.sphaericus.* It seems to be absolutely confined to very shallow waters, amongst rich peaty, partly decaying vegetation, and then is only found when these are acid (in this my observations confirm those of Poulsen, 1929). It has neverybeen present in abundance when I have found it at the margins of lakes, and in these cases the lake was adjoined by patches of peaty marshland which suggests that the species found in the lake are strays from there more usual habitat. This would seem to be mainly very small pool.

Chydorus piger

Madum Sö, 9.9.50., III, a few individuals, probably of this species.

Anchistropus emarginatus

Tarn Hows, 13.8.49., II very scarce; Clay Pool, Wray, 15.8.49., in open very scarce.

This species has been said to be a parasite of Hydra (Berg 1935) This conclusion is not however borne out by the records of its occurence. Most authors record a few individuals, usually on miry bottoms (e.g. Berg, (1929), and it is rare for an abundance of Hydra to be mentioned in connection with the records. I have many times collected large numbers of Hydra without finding a single specimen of Anchistropus. On the other hand on the two occasions when I have found this species I did not find any Hydra in my collections, though admittedly they do occur in both localities. Whilst these observations do not disprove Berg's theories they do cast considerable doubt on them. The special features which are considered as adaptations to parasitism on Hydra would be equally effective as adaptations for attachment to Charales, or coarse algae.

Monospilus dispar

Arresö, 22.8.50., III, one only; Madum Sö, 9.9.50., II, numerous, III scarce.

This species has been often considered as characteristic of muddy bottoms.

It is distinctly rare and most records are of a few individuals only. Scourfield and Harding (1941) say it may occur on sandy or muddy bottoms of lakes, whilst Poulsen (1928) says that it only occurs on sandy lake bottoms.

My two localities have both distinctly sandy bottoms. Apart from this feature Madum Sö, and Arressö have very little in common. Madum Sö is a barren oligotrophic lake with a pH rather constantly in the region of 5. Arressö is highly eutrophic, with very hard water, and is usually markedly alkaline. Thus the species would seem to occur wherever a large habitat contains extensive deposits of undisturbed sand.

Polyphemus pediculus

I have records of this species from 3 lakes and 1 pool in S.Uist; from Loch Ness and a neighbouring pool; from 4 lakes, 4 tarns and a very slow syream in the Lake District; from 3 lakes, and 5 pools in Zealand; and 1 lake in Jutland.

My observations agree with Scourfield and Harding's (1941) rather vague statement that the species occurs near the margins of lakes and in small water channels. It is perhaps somewhat more common where there is sparse floating vegetation, but it may occur well away from any vegetation in shallow water, as at Loch a' Chnoic Bhuide.

I have never found *Polyphemus* in small pools, and it seems to be restricted to waters of large or moderate size. The rarity of the species in the London area and in S.Yorkshire is noteworthy, since there are many apparently suitable habitats. The records suggest though they do not prove that industrial pollution is responsible.

Bythotrephes longimanus

Lake Bassenthwaite, 24.8.49., very scarce; Windermere N.Basin, 24.8.49., numerous, eggs moderate; Windermere, S.Basin, 30.8.49., very scarce.

This has been considered to be arctic-alpine species (Thienemann, 1950); but since it is confined almost absolutely to large lakes such a distribution is inevitable.

Leptodore kindti

Windermere 24.8.49., N.Basin, scarce, large; Frederiksborg Slotssö, II, 25.7.50., very numerous, large; Bastrup Sö, 11.8.50., numerous; Ager Sö, 22.8.50., very abundant, mostly young; Madum Sö, 9.9.50., scarce, but still the most abundant species in the sooplankton.

Frederiksborg Slotssö, and even more the Ager Sö, are very small, shallow lakes. Records from such localities seem to be not infrequent in Denmark and Germany (Berg 1929, Wagler 1937), but the species is never found in any but rater large deep waters in the British Isles. It certainly does not occur in many localities around London which are quite comparable to these Danish localities.

It is generally believed by Danish workers (e.g. Poulsen 1928) that Leptodora is confined to more or less eutrophic, alkaline waters. This is certainly not the case in England as Lake District records show. My record from the Madum Sö shows that it is not true for Denmark either, since as mentioned above this is a very acid, ologotrophic lake.

Distribution of Cladocera within lakes and ponds.

For many species it is impossible to demonstrate any connection between their distribution, and the general nature of the various available waters.

and such connections are rarely clear in any species. On the other hand the distribution of Cladocera within any locality often shows striking localization. Though it is not as yet possible to give a full explanation of the causes of this, certain definite patterns of distribution can be traced, and in respect to these the occurence of species is consistent from locality to locality.

In discussing this problem of localization I shall consider chiefly the littoral species, since I know more about these, and also since they show more striking and clear-cut examples of localization. The principal factors which may give rise to localization within habitats are: food-supply: depth of water; presence or absence of vegetation, and its nature; degree of exposure to wave-action, water-currents etc.; the nature of the bottom deposits; and various biotic factors. I have already dealt adequately with food-supply, and concluded that it is of importance in determining the distribution of the littoral Cladocera. On the possible role of deptch of water I have little information. That it may be important is indicated by Berg's (1938) data for the distribution of *Eurycercus lamellatus* in Esrum Sö. On the other hand it is clear that wide generalizations on this topic are not possible at present, if only because a number of species, as *Latona setifera*, (see above), have very different depth distributions in different habitats. In many cases at least apparent restriction ~~for~~ of a species to certain depths is a result of the action of other factors which happen to be correlated with deptch in some waters, (*Ilyocryptus sordidus*, above). I shall deal with biotic factors in the ecology of Cladocera after I have dealt with distribution between lakes and ponds.

The remaining factors are all to a certain extent inter-related, but fortunately they do not vary absolutely simultaneously, so that it is possible to differentiate their effects to a considerable extent. For Simplicity I shall treat them separately, but I realize that in real habitats the nature of one factor may modify the effects of another. For most of my species I have not sufficient data to show this but it becomes apparent in some of the Chydoridae, and I will deal with it below.

Vegetation is probably the most obvious variable correlated with the distribution of Cladocera and its effects are so obvious and well-known that they seem hardly worth discussing. It must be pointed out however that many correlations between the presence of vegetation and the cladoceran fauna are spurious, the Cladocera being controlled by factors which are not necessarily dependent on the vegetation and may even control this, for instance the nature of the bottom deposits, and the degree of exposure of the shore. The littoral Cladocera can be divided into three principal ecological groups., and it is misleading to treat them all as one group, as is usually done. The first group, of ~~roms~~ forms living mainly at or near the surface film contains only *Scapholeberis mucronata.* As I have pointed out in my notes on that species, vegetation affects it mainly by providing a region in which the water surface is not greatly disturbed. The second group contains the true bottom-living and burrowing forms which are not directly dependent on vegetation, except sometimes as a source of food. The third group consist of the true weed-dwelling species. Any division between these last two groups must be somewhat arbitrary. There are in reality a continuous series of species leading from burrowers such as *Ilyocryptus sordidus*, to such definitive weed forms as *Sida crystallina*, and *Lathonura rectirostris* . A few species are so nearly intermediate in character that they must be considered under both categories. The most important of these if Pleuroxus aduncus, other species, such as Pleuroxus truncatus may be weedforms in most situations, but bottom species in others. However the vast majority of species can be readily assigned to one or other of these two groups. The group of true weed species is the smaller, and consists of Sida crystallina; Simocephalus spp.; Ceriodaphnia reticulate; Ceriodaphnia megalops; Ophryoxus gracilis; Eurycercus lamellatus; Camptocarcus spp.; Acroperus harpae; Alona costata; probably Alona rectangula; Pleuroxus truncatus; Pleuroxus laevis; Chydorus globosus; and Polyphemus pediculus. A few other species, e.g. Drepanothrix dentata, and Anchistropus emarginatus may belong here, but there is no conclusiveevidence in favour of including them. These true weed dwellers are all, to a greater or lesser extent affected by the presence or absence of vegetation, and all are usually most abundant in vegetation zones, though some, as Eurycercus lamellatus and Pleuroxus truncatus, sometimes occur away from all vegetation. Evidence for the association of other species with vegetation is suspect, since the real controlling factor is usually some other feature of the enviroment.

A few remarks may be made on the effect of the general character of the vegetation. Reed-beds in lakes commonly have a very sparse cladoceran population consisting of very few species, a distributional fact that has also been noted by Berg (1929). On the other hand dense submerged vegetation usually has an abundant and varied cladoceran fauna. A few species such as the species of Camptocercus, and to a lesser degree Sida crystallina are rarely found in dense vegetation of any kind; but most species are more abundant in dense vegetation; whilst a few, such as *Ceriodaphnia megalops*, seem to be confined to it.

Certain non-littoral species are sometimes found in vegetation, including *Diaphanosoma brachyurum*, *Daphnia longispina*, and *Ceriodaphnia pulchella*, but they are more normally found in open water, and the individuals in weed-beds can be regarded as strays.

Most Cladocera seem to be unable to withstand any great degree of exposure to wave-action and are also sensitive to other pronounced water movements. In habitats where such water-movements are pronounced the cladoceran fauna is often very sparse, and always limited to a few species, even if there is plenty of vegetation. On the most exposed lake shores no Cladocera are found. On slightly less exposed shores the only species that are at all frequent are *Alonopsis elongata*, and *Pleuroxus truncatus*. The former species is definitely characteristic of somewhat, to moderately, exposed situations, and is only rarely found in sheltered places. On some moderately exposed shores as at Wastwater it may occur in enormous numbers. Part of this apparent preference for fairly exposed localities may be due to its preference for coarse bottom deposits, but this does not fully explain the facts. I have found this species in abundance on fine sand, in and about exposed reed-beds in Blelham Tarn, and Bure Sö, though I have rarely found it on such a bottom in sheltered situations. *Peracantha truncata* is less common in exposed situations, and is only present where there are plenty of algae. In such circumstances it largely replaces *Alonopsis*. Other species that may occur on moderately exposed shores are *Alona affinis*, *Rhynchalonella rostrata*, and *Latona setifera*.

Young individuals of Sida crystallina sometimes occur in these exposed situations, but the adults are more strictly confined to sheltered waters.

An interesting illustration of the effects of exposure is provided by the occurence of planktonic species in inshore waters. In small lakes and ponds, it is usually possible to obtain a fair sample of the plankton within a few feet of the shore, but in large waters it is usually necessary to go out in a boat. In a few instances, however, as near the Wray Castle Boat House, and at one of my stations in the Arresö, I collected in sheltered shallow stations with no vegetation. In these places I obtained quite good plankton samples, containing most of the species present in the lakes in fair numbers. Wesenberg-Lund (1904-1908,1926), in attempting to account for the limitation of zooplanktonts to offshore waters, had put forward the theory that they avoided the littoral zone. This theory was never very convincing, as it was difficult to think of any avoidance mechanism that would prevent species entering the shallow waters of large lakes, whilst allowing the same species to do so freely in smaller lakes. The discovery that these species may in fact enter and flourish in the shallow water in large lakes robs the theory of its observational basis. The rarity of their occurence in the shallow waters of larger lakes is better explained by inability to withstand wave-action, combined with intolerance of vegetation, which does seem to be characteristic of most plankton species.

The factor which results in the most detailed localization of littoral Cladocera is the nature of the bottom, though this is only important for predominantly bottom-dwelling forms. Table 19 shows the number of habitats in which I have collected specimens of each of the more characteristic bottom species, grouped according to the nature of the bottom deposits. I have also included a few non-bottom-living species for comparison. The table is self-explanatory and few further comments are necessary. The non-bottom-living spefies show no obvious association with the nature of the bottom deposits, but such an association is marked in almost all the bottom-living species. An exception to this statement is provided by Acantholeberis curvirostris which though spending much of its time on the bottom does not seem to be much influenced by its nature. In considering the nature of the bottom deposits I have paid more attention to its physical than to its chemical nature. As I have pointed out in discussing Ilyocryptus sordidus, the physical nature of muds and sands does seem to be of more importance than the chemical nature. An exception is provided by habitats with very large quantities of vegetable detritus or decaying vegetable matter. As can be seen from the table, these conditions can have a pronounced effect on the fauna. The small group of species which are almost absolutely confined to decaying vegetable matter or its immediate vicinity are particularly interesting as examples of extreme habitats specialization. In reading the table it must be borne in mind that only the major features of the habitats have been considered. In many cases a bottom of consolidated sand will contain minute patches of silt. Species such as Pleuroxus uncinatus occuring in these patches must be included in the sand population, since it is not possible with the available collecting methods to distinguish the populations of such silt patches from the surrounding sand. In most instances such sources of error have not seriously affected the results though making them less precise, but for this

P.uncinatus the data as given in the table do give a false impression. All the sandy habitats in which I have found it contain such small silt patches and the numbers of individuals which I found in such habitats were usually less than those I found in more uniformly silty areas. Thus the apparent dominance of sandy habitats in the records is almost certainly fallacious. When such possibilities of error are allowed for the table does provide a good summary of the relation of the species concerned to the nature of the bottom deposits.

As I have already indicated certain factors tending to localose the distribution of littoral Cladocera are not completely independent in their effects. My collections have not been sufficiently extensive to provide many good examples of this, but the effect of exposure in increasing the range of bottom materials on which A.elongata may occur, and in allowing the same species to flourish in reed-beds may be noted. Similarly an abundant supply of algae allows Pleuroxus truncatus to become established on exposed shores from which it is normally absent. The presence of extensive sandbeds allows Alona affinis to become established in exposed places where it certainly would not occur if the bottom were mainly stony. Each of the various factors which I have considered is important in determining the distribution of Cladocera, but the presence or absence of any species in any particular habitat depends on the resultant of all the enviromental factors. Thus a species may fail to establish itself in a station with suitable bottom conditions if the other conditions are unsatisfactory; whilst it may be present on an unusual type of bottom if the other conditions are all favourbable. Such exceptional occurences do not disprove the idea that the nature of the bottom deposits, for instance, is of crucial importance in Cladoceran ecology, but merely underline the fact that the animal responds to its environment as a whole rather than to its individual components.

The cladoceran fauna and the general character of the water-body.

Whilst it is easy to find a clear pattern in the localization of species of Cladocera within water-bodies, it is not usually possible to correlate the general nature of a water-body with its overall cladoceran fauna, a difficulty which has been commented on by Gurney. This lack of correlation is least pronounced for the smallest water-bodies. In these the number of possible habitats is very limited, and also conditions are often extreme, so that it is possible to recognize a number of distinct types of small waters, such as 'Daphnia' pools and peat-bog pools, which tend to have a uniform and characteristic fauna. For most types of water-body such correlations are largely non-existent, lakes of the most diverse characters having very similar faunal lists. Thus with the exception of Alonopsis elongata the commonest species found in Ennerdale are also amongst the commonest the commonest species found in the highly eutrophic calcium rich Esrum Sö, whilst a comparison of the faunal lists for the larger lakes in the English Lake District suggests strongly that most of the differences between them are the result of collecting accidents, whilst the few real differences between them cannot be correlated with any known general features of the lakes concerned. This was Gurney's (1923) opinion, and is the inevitable impression given by collecting in the Lake District, or by perusal of the Scourfield Ms. Nevertheless as certain authors, Poulsen (1928) in particular, have claimed to show that most Cladocera are correlated in their occurence with certain general features of the water-bodies they inhabit, as for instance pH., the evidence must be examined in more detail.

The principal factors which are likely to have an effect on the fauna of a water-body as a whole, rather than on limited habitats within it are: temperature; light; pH, and the associated hardness or softness of the water; the trophic degree of evolution of the water-body; the size of the water-body; its permanence; and its lenitic or lotic nature.

Of these I have already dealt with temperature and light. The latter can scarcely be of much general importance since it varies so slightly from habitat to habitat. Temperature may be important in controlling the distribution of a few species, such as *Moina spp.* but seems to have little connection with the distribution of most Cladocera.

Poulsen (1928), from his studies on the distribution of Danish Cladocera, came to the conclusion that the acidity or alkalinity of the water of the locality was of great general importance in the controlling distribution of Cladocera. On the other hand Brehm (1933), and Pacaud (1929) both conclude that, except for a few species the Cladocara are indifferent to pH. within wide limits. As will be seen from my notes on the individual species my results agree with the opinions of Brehm and Pacaud and are totally opposed to those of Poulsen, which seem to me to be the result of over-hasty generalization from inadequate data. Indeed I am convinced that even the limited role that Pacaud allows to pH. is an exaggeration. Some species, such as *Macrothrix laticornis*, which Pacaud thinks are confined to waters which are at least slightly acid, occur in hard alkaline to neutral water in the London area. I think that apart from the few acidophilic species (such as Acantholeberis curvirostris, Streblocerus serricaudautus, Chydorus ovalis, and in my opionion, Simocephalus serrulatus, and Ceriodaphnia quadrangula, the Cladocera as a whole are distributed independently of pH. or of the hardness of the water. It is particularly noteworthy that certain species which have been considered by Danish workers to be characteristic of hard-water lakes, such as Daphnia cucullata, and Leptodora Kindti, occur even in Jutland in rather acid lakes with soft-water. On the other hand my evidence is consistent with a very few littoral Cladocera, such as Camptocercus spp., being calciphiles, though even in these cases the conclusion is not certain (C.rectirostris, for instance has been recorded from several of the Lake District lakes).

Whilst I do not think that pH. is of any great importance generally in cladoceran ecology there are one or two peculiar facts that require some explanation. It is noteworthy that very alkaline, hard-water localities often have a less rich fauna than more acid localities, especially in respect of the rarer species. Thus the well-worked Esrum Sö has a much less imposing faunal list than Lake Windermere and Esthwaite Water have. In small habitats the richness in species of acid waters is very striking. Thus I have recorded 9 species from Hjorte Söle and II for the Loch Skiport Hill Pool, though from equally small waters with hard-water I have rarely obtained more than three of four species. Several species which are otherwise rare in small waters occur these acid localities, e.g. Lathonura rectirostris, Acroperus harpae, Bosmina longispina. Thus a low pH. in some way seems to compensate for small habitat size.

A feature that I find it impossible to explain is the almost complete absence of the pond species of Daphnia from the mountainous, non-limestone areas of the British Isles. This is certainly not due any rarity of small polluted pools, which are as sommon in these areas as in many other regions where such species occur. The distribution suggests that the pond Daphnias need water with a fairly high calcium content, and a pH of about 7, a conclusion which has been reached by some workers as Vier hoever (1935), and Soröm 91926) on the basis of their experiences with cultures. Unfortunately the distributional facts do not support this theory, Pacaud has found D.'pulex' in pools with a pH. as low as 4.9-5.5. Such records are exceptional, but it is not very uncommon to find D.obtusa in rather acid waters. I have collected this species from the Curling Ponds on Putney Heath, which are definitely acid, moss-bottomed pools. It also occurs in a pond at Golder's Hill, which at the time of my visit had a pH range of 5.0 to 6.4, and a temporary hardness as low as 2.9 mgms. ~~Calo3~~ $CaCO_3$ per litre. Thus there seems to be no reason why this species at least should not occur in such areas as the Lake District.

The Cladocera as a group do not seem to be affected by the trophicity or degree of evolution of lakes, (as Gurney also maintained (1923)). A few species such as Holopedium gibberum are never found in highly eutrophic lakes. Even with these species the correlation with oligotrphy is not very well-marked. H.gibberum is not found in many primitive lakes; but it occurs in abundance in the comparatively evolved Rydal-water. The intolerance of theis species for high calcum concentrations (Thienemann 1926) gives a more probable explanation of its distribution; this intolerance would ensure its absence from eutrophic lakes. A species which can ~~trkx~~

truthfully be said to occur most abundantly in non-eutrophic waters, and whose distribution does seem to be correlated with the trophic degree of lakes as such is *Alonopsis elongata*. It is by no means clear how the trophicity of a lake can affect the occurence of such a littoral form, but all more obvious limiting factors fail to account for the distribution of this species in a satisfactory manner. The avoidance of eutrophic conditions is not quite absolute as Berg's records from Sorö Sö shows, but it is almost so, and certainly needs a special explanation.

Several Cladocera have been considered to be more or less strictly restricted to eutrophic habitats, but examination of the evidence shows that the hypothesis must be abandoned for most of them, including *Leptodora kindti and Daphnia cucullata* (see above). A Few species remain which seem at present to be characteristic of eutrophic waters. One of these is *Ceriodaphnia dubia*, though its comparative rarity makes the conclusion a little uncertain. More certainly restricted to more or less eutrophic habitats are the species of *Camptocercus.* These are apparently not uncommon in the eutrophic lakes of Zealand, but are rarely found in the less eutrophic lakes of N.England. Those lakes in the lake district for which *C.rectirostris* has been recorded are amongst the most eutrophic. It has been pointed out above that competition with *Alonopsis elongata* may be a factor involved in determining this distribution, though it is difficult to see how the trophicity of a lake could influence the coarse of such competition.

These few species which do seem to be affected by the trophicity of the water-body are definitely exceptional, and do not affect the statement that the group as a whole is distributed independently of the trophic nature of the environment, as such. It is not improbable that even the few species whose distribution at present seems to be controlled by trophicity are actually influenced by some other simpler factor.

Of all the varying features of lakes and ponds, size is the most obviously associated with differences in the cladoceran faura. A glance at any series of faunal lists shows that the larger the water-body the greater the number of species recorded from it, if habitats comparable in other respects are chosen for the comparison. This is in large part due to the greater variety of habitats provided by the larger water, but this is not the full explanation, since there are usually more species in the same general variety of habitats provided by the larger water, but this is not the full explanation, since there are usually more species in the same general type of habitat in the larger water-bodies. This is clearly shown by table 20, which gives the average numbers of species obtained per collection in the weed-zone in localities of different sizes in Denmark. Similar figures could be obtained for English localities but for my results they would be complicated by seasonal differences, whereas all the Danish localities were collected in the same season.

A considerable number of species are rarely if ever found in very small waters, except where these are semi-lenitic. The most important of these are *Sida crystallina*; *Diaphanosoma brachyurum*; *Bosima obtusirostris* *Lathonura rectirostris*; *Eurycerous lamellatus*; *Alonopsis elongate*; *Acroperus harpae*; *Polyphemus pediculus*; *Bythotrephas longimanus*; *Leptodora kindti*; and *Holopedium gibberum*. Many other species, such as

Daphnia hyaline; *D.cucullata*; *Ceridaphnia quadrangula*; and *Ceriodaphnia pulchella*, though sometimes found in very small waters are characteristic of lakes. The lower limit for the usual size of waters occupied varies from species to species, and is also affected by other features of the habitat as by the calcium content of the water(thus *B.obtusirostris* and *Alonopsis elongata* both occur in smaller waters where these are acid than they do where these are alkaline). Nevertheless it is clear that for all a locality must be of minimum size for them to become well-established, unless conditions are otherwise unusually favourable.

On the other hand few species seem to be restricted to small water-bodies. Most of these, as the pond species of *Daphnia* have closely related species which normally live in larger waters. These species are most probably excluded from the larger waters by competition. That pond species of this genus can live in large water-bodies is shown by exceptional records, such as that of *D.magna* for the King George VI Reservoir, Middlesex. Other species which appear to be largely restricted to small waters, are in reality restricted by the need for suitable micro-habitats. Where these are present they occur in large lakes. Such species include *Ceriodaphnia megalops* and *Ilyocryptus sordidus*. Very few remain when these two categories are removed, indeed I can find no certain instance, amongst the species which I have collected of a species which is restricted to small habitats and in which the distribution is not probably either the result of competition or the result of lack of suitable micro-habitats in the larger water-bodies.

Temporary pools often have a very restricted cladoceran fauna, the only species which are commonly found in them being species of *Daphnia*. *Chydorus sphaericus* though the most frequent of all Cladocera in permanent habitats is very rare in temporary pools. This faunal restriction is not due solely to the impermanence of the habitat. The Thetford Meres, which are at the most only semi-permanent, have a very rich fauna comprising such species as *Simocephalus vetulus*, *Ilyocryptus sordidus*, *Pleuroxus truncatus*, and *Chydorus sphaericus.* Similarly the Apus pool at Godshill ~~God's Hill~~ contains such species as *Macrothrix hirsuticornis* and *Alona elegans.* All these species are comparatively unpolluted, and the Thetford meres are large, and probably disappear mainly as a resulf of underground drainage, rather than evaporation. Thus they are not so extreme in their conditions as most temporary pools, and probably are more constant in their chemical nature. It seems probably that the restricted faunas of temporary pools are due rather to associated environmental condiitons than to the impernanency, of the environment.

Cladocera are very rarely found in any but the slowest rivers and streams, almost the sole exception in this respect being *Eurycercus lamellatus*. This is not easy to understand, since a number of species, wuch as *Latona setifera* and *Alonopsis elongata*, occur within lakes in places with considerable water-movement. On the other hand very slow rivers, river and stream pools, backwaters, and other habitats which I have classed as semi-lenitic may have a considerable cladoceran fauna, though in my experience open-water species are usually absent with the single exception of *Daphnia longispina*. Weed-dwelling and bottom-living species flourish, and in respect to these the fauna is usually comparable with similar habitats in lakes. It is noteworthy that a number of species which are more normally found in large or moderately large habitats may occur in very small semi-lenitic habitats. Such species include *Lathonura rectirostris*, *Eurycercus lamellatus*, and *Acroperus harpae*.

A feature which is difficult to assess, but which may be of considerable importance in cladoceran ecology is the constancy of the environment. The greater number of species found in large waters, the apparent effects of acid water and semi-lenitic nature in allowing a number of species to live in smaller habitats than are usually inhabited by them, and the fact that a number of species which are perfectly capable of surviving periods of drought are nevertheless rarely found in temporary pools, all suggest that some degree of environmental constancy is beneficial to many species. Macan (1950) has suggested that such environmental constancy may be important in determining the distribution of aquatic Gastropoda.

Biotic factors in the distribution of Cladocera

I have not been specially concerned with biotic factors in my survey but my observations do present a few features of interest. As I have attempted to bring out in the preceding discussions competition between species is probably an extremely important factor in determining the distribution of Cladocera, and I need not enlarge this further here. In view of the tendency of many recent workers to focus there attention mainly on closely related species, it may be stressed that this competition in the Cladocera is between forms with similar ecology, irrespective of their systematic position. Thus the competition between species of Moina and the pond species of Daphnia is just as important as the competition between these species and the lacustrine species of Daphnia. Similarly Bleuroxus truncatus appears to compete with Alonopsis elongata though it is only remotely related to it. There is also some evidence that competition between Cladocera and members of other groups may be important in some circumstances. Most important of these possibly competing groups is the Copepoda. In very small ponds it is usual to find that the dominant Entomostracan is either a single species of Daphnia or Chydorus sphaericus, or one of the copepods, Cyclops strenuus, Acanthocyclops bisetosus, Acanthocyclops bicuspidatus, Acanthocyclops languidus, or A. vernalis. Often if copepods are present there are no Cladocera, and vice versa, though sometimes they occur together. In my experience when this occurs either the cladoceran or the copepod is scarce at any one time, though the relative numbers may change from time to time. These observations strongly suggest competition. That such competition is probable is borne out by examination of the gut-contents. I have examined the gut-contents of individuals of Cyclops strenuus from a number of flourishing populations. In each instance the guts were filled with small nannoplanktonic algae, of the same type as those consumed by species of Daphnia. It is not possible to demonstrate such competition in the more complex conditions of larger waters, but it doubtless occurs since a number of lacustrine copepods, such as the species of Diaptomus feed on small algae and must thus consume part of the food-supply which would otherwise be available for the Cladocera.

A very considerable number of animals prey on Cladocera, and a few seem to specialize on such food. Amongst predators which I have observed are Stantor (on the smallest species, see also Birge (1918)); Hydra spp.; Asplanchna; Chaetogaster diaphanus, which seems to be a specialized feeder on Entomostraca; Acilius larvae; Chaoborus larvae; a species of Tanypod; and Orthotomid; tadpoles; and various fishes. Scourfield records net-spinning Chironomidae as predators; whilst many other insect larvae have been observed to feed on Entomostraca on various occasions. Of all these predators only the tadpoles and the fish seriously affect the numbers of Cladocera present in any habitat. (It is possible that Chaoborus may also have profound effects on the abundance of Cladocera, since collections containing many individuals of Chaoborus rarely contain many Cladocera). Other conditions characteristic of Chaoborus habitats, such as the shortage of oxygen, would also result in reduced numbers of Cladocera, so that this scarcity cannot be certainly ascribed to predation. Tish certainly have a profound effect on the Cladoceran fauna. Lake reed-beds containing swarms of young fish have few Cladocera. In two ponds which I have investigated in London, the Brent Decoy Pond and the Statue Pond, a large increase in the numbers of fish present was followed by the complete or almost complete disappearance of Cladocera, though the cladoceran populations showed no signs of dying out previously.

Parasites and epibiotes may also be important in determining the abundance of Cladocera. Epibiotes are very common and varied. Amongst those which I have observed most frequently are *Colacium* spp.; *Amoebidium parasiticum*, a species of doubtful affinities which has been overlooked in the British Isles, though it is very common; *Achnanthes* spp.*Cocconeis* sp. various Vorticellidae; *Bicosoeca* spp.: various Suctoria; *Proales daphnicola*; and *Brachionus urceolaris*. With the exception of *Colacium* none of these seems to injure the 'host' in any way, except when so extremely abundant as to hinder locomotion or feeding by purely mechanical interference. *Colacium* when abundant does seem to be associated with enfeebled populations; but I cannot be sure whether the enfeeblement is due to the *Colacium* or the abundance of the *Colacium* is only possible as a result of the enfeebled condition of its 'hosts'.

I have observed a number of endoparasites of *Daphnia*, including various microsporidians, a rod-like bacterium, and nematodes. All these are fatal to moth individuals, and may decimate a laboratory culture. They are however extremely rare in nature, so that their actual importance in controlling natural populations is probably slight.

General discussion.

The ecology of the Cladocera cannot readily be expressed in a simple scheme of reactions to one factor or group of factors. In this they differ markedly from such groups as the Corixidae (Macan 1938), and the terrestrial Mollusca (Boycott 1934), but are comparable with the aquatic

Gastropoda (Boycott 1936, Macan 1950). A few exceptional species as Moina spp. and Acantholeberis curvirostris are rather strictly confined to one particular type of habitat, but for the group as a whole it is only possible to say that the number of species present in a habitat depends on whether it is generally 'good' or 'bad'. However, as I have endeavoured to show it is possible, for many species, to discover minute features of ecology characteristic of the species, which do not, however, show sufficient regularity, as between species, to give the group as a whole a regular pattern of ecological preferences. The ecological differences between some species still defy analysis (as for instance differences between Daphnia obtusa, and D. curvirostris), but there is no reason to believe that such differences will not ultimately be found. It may be suggested that other groups such as the aquatic Gastropoda which at present defy ecological analysis will also be found to show small, non-systematic differences in ecology, such as appear to characterise the Cladocera.

A much discussed problem in recent years is that of the ecological relationships of related species. It has been assumed that closely related species must have generally similar requirements and so must compete if occupying the same habitat. It is argued that, except in very special circumstances, they can only continue to occur together if they show some ecological differentiation, for instance in regard to food-supply. This theoretical conclusion has received strong support from the experimental work of Gause (1934) and of Park (1948). These workers showed that under experimental conditions closely related species of Paramoecium and Tribolium cannot persist together indefinitely in the same habitat. It seems to me to be at least very doubtful whether this need be so in the more complex conditions normally occuring in nature. Lack (1944, 1946) however has shown that closely related species of birds occupying the same habitat are almost invariably slightly different in their ecology. Elton (1946) has remarked on the fact that in small habitats a much larger proportion of genera are repsented by a single species than is the case in the fauna of the whole district in which they occur. He takes this as evidence for competition between related species and as support for Gause's contentions. However Williams (1947) has criticized Elton's conclusions, and shown that they are based on faulty analysis. According to hima higher proportion of related species are found together in small habitats than would be expected on the basis of chance alone.

My collections indicate, that as far as the Cladocera are concerned, closely related species are in fact found together much more commonly than would be expected on the basis of chance occurence. Thus it is very usual to find two species of *Daphnia* in the same habitat, whilst I have on several occasions found as many as three species living together; e.g. in the gull-pond at the zoo, where I have found *D,magna*, *D.curvirostris* and *D.obtusa* together, and in the Leg of Mutton Pond, where I have found *D.pulex*, *D.obtusa*, and *D.curvirostris* together. Similarly *Simocephalus vetulus* and *S.exspinosus*; *Ceriodaphnia reticulata* and *C.megalops*; *Alona affinis* and *Alona quadrangularis*; and *Chydorus ovalis* and *C.sphaericus* are commonly found together in the same limited habitat.

In some cases as the two *Simocephalus* species it is possible to point out features in their biology which would greatly reduce competition, but this is not so for most of these groups of species. Again there are no readily apparent ecological differences between such species as *Diaphanosoma brachyurum* and *Ceriodaphnia pulchella* which would prevent them competing when they occur together as they often do. It is not of course impossible that such ecological differences may yet be discovered but this seems to be very unlikely as so few relevant aspects of their biology remain uninvestigated. At the moment it is safe to say that whilst the species of this group show considerable ecological differentiation, this is not in all cases sufficient to explain the persistence of several closely related species in the same general habitat. It would seem that in natural conditions the selective advantages and disadvantages of one species over another may balance out over periods of time, so that the resultant selection pressure is effectively neutral. It is possible that this is a special feature of cladoceran distribution, resulting from such features as the plasticity of their reproduction; but there is at present little reason to suppose that it may not be general amongst invertebrate groups.

General Summary

This thesis is concerned with showing the roles played by various factors in the ecology and distribution of Cladocera.

It has been shown that as a group the Cladocera have a very high thermal resistance. It is unlikely that the direct lethal effects of high temperatures are of any importance in determining the occurrence of most Cladocera.

The occurrence of thermal races is apparently a common feature of cladoceran physiology. This still further reduces the probability that mortality due to high temperatures is an important controlling factor in cladoceran distribution.

Most W. European Cladocera can survive at temperatures near to 0°C., and many can reproduce at such temperatures. A few species however, such as Moina spp die at temperatures considerably higher than 0°C.

The number of young reproduced by cladoceran individuals in a given time depends on the frequency of moulting, and the number of young produced per instar. Both of these are affected by various environmental conditions, but, contrary to the opinions of some American workers they do not usually show any appreciable variation with the age of the individual.

Temperature causes an increased frequency of moulting, and the increase in frequency is of the same order in the three species investigated. The difference observed may be correlated with the seasonal occurrence of the species, but this is not certain. Instar length appears to be fairly uniform at any given temperature, throughout the genera Daphnia and Ceriodaphnia.

The effect of temperature on egg-number varies from species to species to species. In some species egg-number is higher at 27°C than at 18°C but in others it is lower. These differences seem to be associated with differences in the seasonal occurrences of the species.

The age of maturity and the longevity of individuals also vary with the temperature. They are roughly but not absolutely correlated with differences in length of instar.

Light, food and crowding have no significant effects on frequency of moulting.

Darkness, shortage of food and crowding all reduce egg-proportion. Their effects vary from species to species, but show no significant interaction with temperature.

Darkness and shortage of food may cause postponment of maturity by one or more instars.

Food has no significant effect on longevity.

The nature of the available food-supply is very improtant for non-planktonic Cladocera. Almost all of these can be clearly classed either as detritus feeders, or as algal feeders. Their occurence and abundance in nature are correlated with the amounts of these potential foods available. There is some evidence that a few species at least feed selectively the selective mechanism probably being largely choice of suitable feeding sites.

It is less easy to reach definite conclusions on the food of planktonic Cladocera; but a combination of various methods of investigation indicates that most of these are primarily feeders on minute algae. There is no evidence for selective feeding in these species.

The size of food-particles taken by the Cladocera of large waters is normally less than that of those taken by the Cladocera of small waters. This however, may be merely consequence of the greater relative abundance of very small algae in the plankton of larger waters.

The size and nature of many of the food-particles taken, and observations of feeding in living individuals suggest that many species at least are not accurately described as filter-feeders, though the Sididae and Daphniidae may be termed vortex feeders.

Notes are given of the outstanding features of the ecology and distribution of the species of Cladocera which I have encountered in field-collecting.

Factors acting within specific habitats in a water-body are important in determining the occurence of many species, but general features of the water-body are of considerably less importance.

The presence of vegetation is important for many Cladocera, but many species which appear to be associated with vegetation are really dependent on other environmental features, such as the nature of the bottom.

Exposure of a habitat to wave-action or water-movement greatly restricts the number of species that can occur in it, though a few species are most often found in more or less exposed habitats.

With very few exceptions true bottom-living Cladocera are closely associated with a specific type of bottom deposit. The physical nature of such deposits is more important than their chemical nature. Weed-dwelling species are not associated with any particular type of bottom.

The effects of vegetation, exposure, and the nature of the bottom, may be modified by other environmental factors.

Most general features of water bodies such as pH., and trophicity, are not of great importance in the ecology of the Cladocera, except for a few species. Size of habitat is, however, of importance, larges habitats being favourable to a greater number of species. Few species are restricted to small water-bodies, and the small size of the habitat is not in itself certainly favourable to any of them.

Cladocera are rarely found in lenitic environments, but semi-lenitic environments, even when of small size, seem to be favourable to many non-planktonic species.

It is suggested that environmental stability is an important factor in Cladoceran ecology.

Competition between species seems to be important in determining the distribution of many species of Cladocera.

There is evidence of competition between some Cladocera and some Copepoda.

Numerous animals prey on Cladocera, but only fish are of any importance in controlling their numbers.

There are numerous epibiotes of Cladocera, but most of these are quite harmless. The majority of endo-parasites are very harmful but they are extremely rare and so probably not of any great importance in cladoceran ecology.

Whilst it is impossible to formulate any simple general rules for the ecology of Cladocera, each species seems to have well-defined ecological requirements.

Related species of Cladocera commonly occur together in the same environment, and do not always show, ecological differentiation of a sort which would prevent competition. Thus the contention that two species with the same ecological requirements cannot survive together indefinitely does not certainly apply to Cladocera, under natural conditions.

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Table 19. Distribution of Cladocera in relation to dominant bottom deposits.

Species	Number of habitats in which the species occured						
	Rocky to Gravelly	Sandy	Sandy-Silt Silt and Soil	Detritus Covered	Muddy	Thick Decaying Vegetation	Mosses
Alonopsis elongata	14	12	7	1	1	—	—
Latona setifera	2	1	2	—	—	—	1.
Macrothrix laticornis	—	13	2	—	—	—	—
Rhynchalonella rostrata	—	8	1	1	—	—	—
Alona quadrangularis	—	12	1	—	2	—	—
" affinis	2	24	13	5	4	—	—
Monospilus dispar	1	2	—	—	—	—	—
Pleuroxus aduncus	1.	10	6	—	2	1	—
" trigonellus	—	3	3	1	1	—	—
" uncinatus	—	15	13	3	—	—	—
Ilyocryptus agilis	—	1	1	1	—	—	—
Drepanothrix dentata	—	1	2	1	—	—	—
Pleuroxus laevis	—	1	3	3	1	—	—
Alonella exiqua	—	—	2	1	1	—	—
" excisa	—	—	4	3	—	1	3
" nana	—	—	2	—	1	—	1
Streblocerus serricaudatus	—	—	3	—	—	—	1
Acantholeberis curvirostris	—	2	2	—	—	—	5
Alona costata	—	—	1	1	1	—	—
" rectangula	—	—	1	1	3	—	—
Grapt. testudinaria	—	—	4	—	5	—	1
Leydigia leydigi	—	2	4	1	7	—	—
" acanthocercoides	—	—	—	—	2	—	—
Ilyocryptus sordidus	—	—	1	1	12	—	—
C-daphnia laticaudata	—	—	2	—	1	7	—
" rotunda	—	—	—	—	(2)	2	—
" setosa	—	—	—	—	—	2	—
Oxyurella tenuicaudis	—	—	—	—	1	1	—
Alonopsis ambigua	—	—	—	—	1	2	—
Pleuroxus truncatus	4	13	29	2	7	—	5
Camptocercus lillj.	—	2	1	1	1	—	—
" rectirostris	—	1	1	—	—	—	1
Sida crystallina	6	20	19	6	3	—	—

The horizontal lines mark out groups of species with roughly similar distributions. The last four species are not primarily bottom forms.

Table 20. Size of water-body and number of species per collection in weed-zone of Danish lakes and pools.

Area (sq. m.'s) *	Number of localities	Average number of species per collection	Extreme numbers of species per collection
> 1,000,000	5	6·04	1 and 9
100,000 to 1,000,000	5	6·92	1 and 10
50,000 to 100,000	3	7·90	3 and 13
10,000 to 50,000	5	3·80	1 and 16
5,000 to 10,000	5	4·40	2 and 8
1,000 to 5,000	4	3·70	0 and 7
< 1,000	5	3·00	1 and 4

* It is impossible to determine lake volumes directly; but, since the depths vary around increasing modes from smaller to larger lakes, areas can be used as a first approximation.

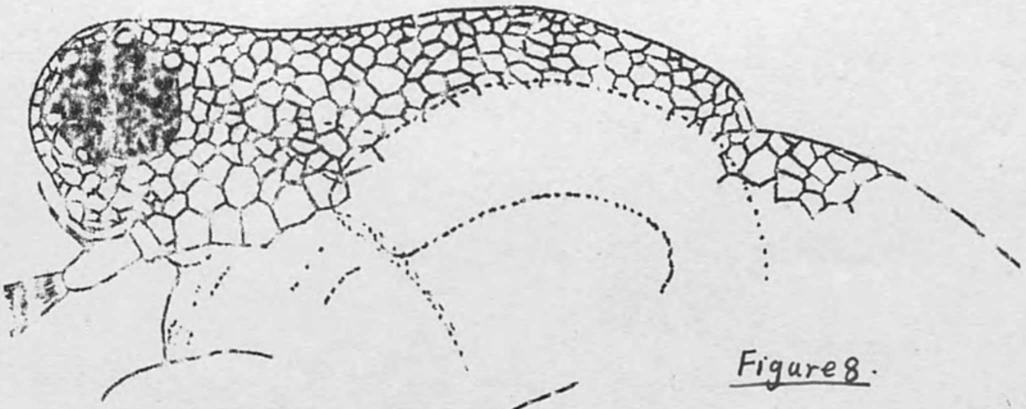


Figure 8.

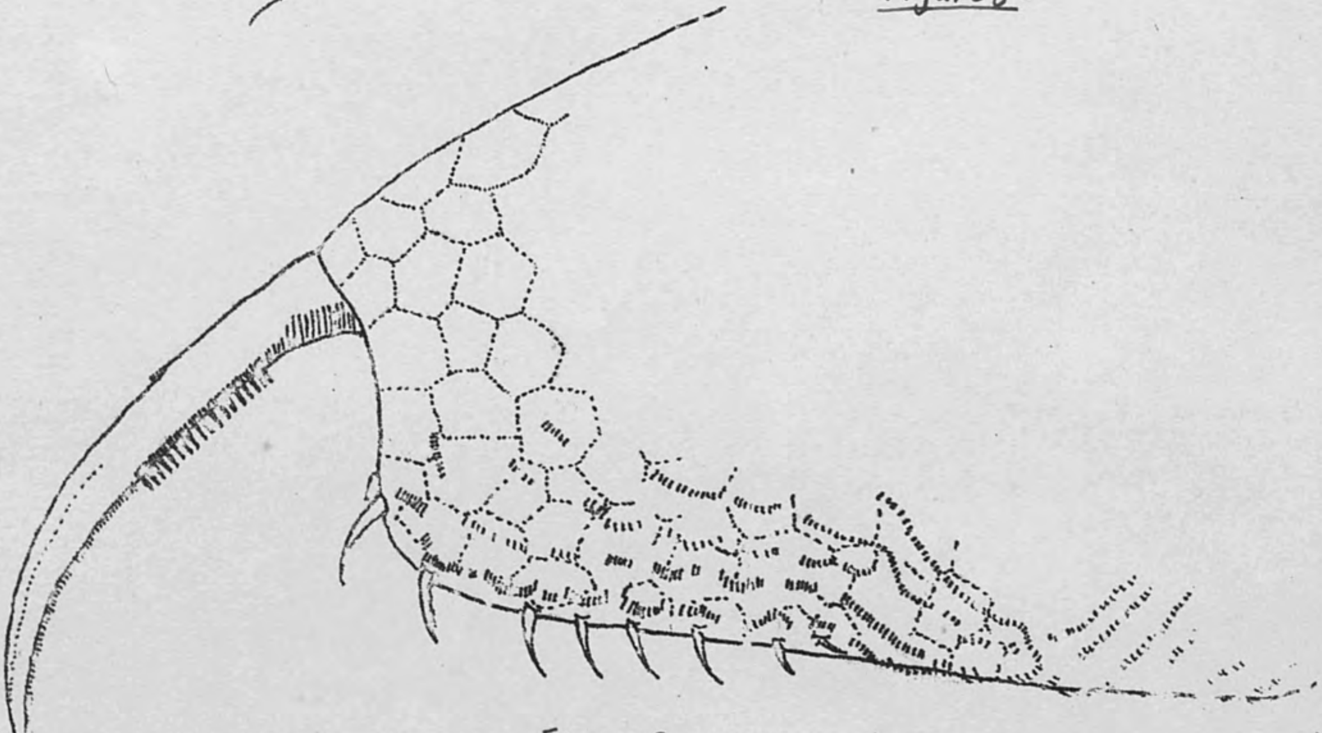


Figure 9.

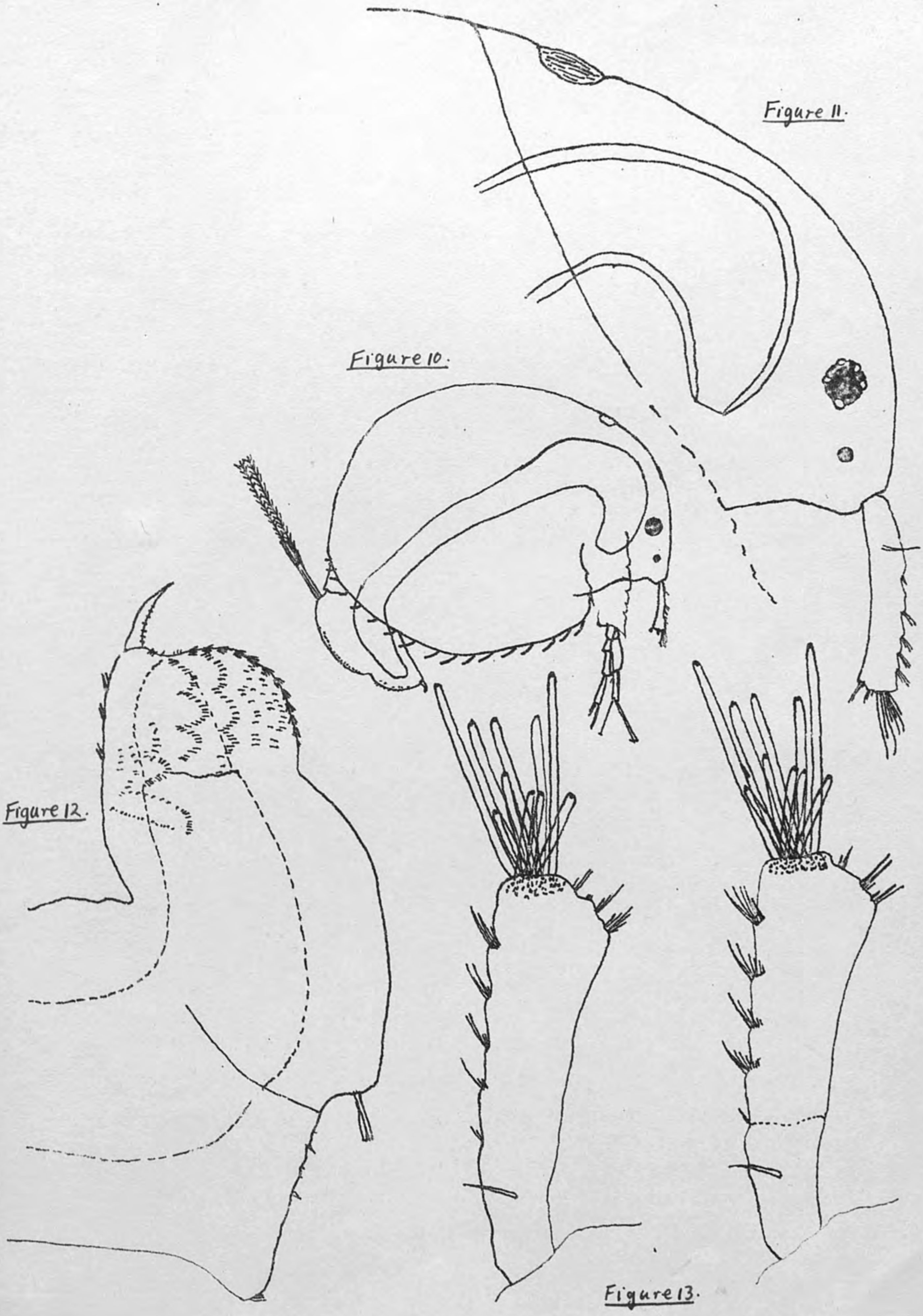


Figure 11.

Figure 10.

Figure 12.

Figure 13.

Appendix 1. The gut-contents of various Cladocera.

Sida crystallina

8.8.49. Boat Dock, Low Wray Bay.

Mainly algae, where no comments membranes only: *Sphaerocystis* scarcely digested; *Ankistrodesmus* some undigested; large *Cosmarium*, chloroplasts; small *Cosmarium*; large *Navicula*, doubtfully alive; *Gomphonema*; *Eunotia*; *Nitzschia*, partially digested; minute needle diatoms, digested; minute diatom undigested; *Oscillatoria splendida* and other species.

8.8.49. Blelham Tarn.

Very sparse gut-contents, mainly algae: ? *Sphaerocystis*, almost undigested; small *Cosmarium* and *Navicula*, some empty.

8.8.49. Blelham Tarn, outside reeds.

Guts brown, much detritus. Many diatoms particularly *Achnanthes* and Navicula; many individuals of a small *Cosmarium*; all partially digested. Few specimens of *Sphaerocystis* and *Scenedesmus*, not digested.

8.8.49. Blelham Outflow.

Staurastrum nr. anatinum (with processes to 10μ) , several membranes only; large thick-walled *Cosmarium*, 2 undigested; small *Navicula*, partly digested; fragments of filamentous algae and plants, digested. In the food-grove there was a large *Closterium* and a large *Navicula*.

12.8.49. Low Wray Bay.

Gut-contents of individuals examined contained some plant fragments and detritus but were mainly algal. The principal algae were *Botryococcus braunii*, which was partly digested and almost the only contents of the guts of some individuals; *Cocconeis*, *Cyclotella* and other diatoms, membranes only; fragments of filamentous Algae.

16.8.49. Borran's Field.

Scarcely any detritus. 3 species of *Staurastrum* in large numbers, one near *S.paradoxum*, the others armless, all digested posteriorly; large *Cosmarium* numerous, little digested; medium *Cosmarium* numerous, completely digested posteriorly: small *Cosmarium*, numerous, mostly digested posteriorly; *Gonatozygon brebisonii*, very numerous, all digested posteriorly. Less important were *Cosmarium margaritaceum*, undigested; ? *Botryococcus*, very little digested; *Ankistrodesmus*, numerous, scarcer and partly digested posteriorly; *Pediastrum*, whole colonies, only found anteriorly.

28.8.49. Wiseen.

Micrasterias radiata, membrane; *Staurastrum* one only, partly digested; *Botryococcus*, enormous quantities, at most only partly digested;? *Cocconeis*, many fragments; very fragmentary remains of *Volvox*.

28.8.49. Wray Mires.

Ankistrodesmus, some appear living; small *Cosmarium*, mostly membranes only; small *Staurastrum*, membranes only; small diatom; *Botryococcus* fair amount, perhaps partly digested; a little *Merismopedia*.

12.10.49. Little Stanmore 2.

Mainly algae especially *Botryococcus*; some detritus.

4.7.50. Highgate 3.

c30% detritus, particles to over 30µ, remainder Algae and their remains. *Scenedesmus*, moderate numbers digested; *Kirchneriella* and *Nephrocytium*, partly digested; *Cyclotella* and *Chrysococcus* absent or unidentifiable posteriorly; *Chrysophycean*, mostly digested.

25.7.50. Frederiksborg Slottssö.

Almost wholly algal, c 50% *Microcystis*, partly digested; also 'orange' Scenedesmus abundant; *Achnanthes*, very abundant, mostly digested; various thecate flagellates, abundant, mostly digested, and others.

22.7.50. Teylgaard Sö.

Mainly very fine debris. A few diatoms as *Asterionella*, empty.

25.7.50. Esrum Sö.

C 50% detritus, very fine to very coarse (long pieces to c.200μ); remainder algae especially *Achnanthes*, mostly digested; *Amphora* some digested; ? *Cyclotella*, digested; *Trachelomonas*, mostly digested; ? *Nephrocytium* digested; and *Scenedesmus*, scarcely digested. There was a little *Botryococcus*.

9.8.50. Frederiksborg Slotssö.

Detritus 3μ to 40μ in length, but mostly less than 20μ. The available algae were scarce, and the population was far from flourishing.

The predominance of *Botryococcus* in many of these records is a spurious effect, due to its abundance in the habitats, and its extreme indigestibility. The term "partly digested" used in connection with this alga merely means that sufficient digestion had occured to produce a change in appearance of the colony.

Diaphanosoma brachyurum

8.8.49. Blelham Tarn.

Guts choked with very fine particles, ? Bacteria.

16.8.49. Codale Tarn.

Guts choked with a mass of very fine unidentifiable particles. A few *Dinobryon* cases.

19.8.49. Blelham Tarn.

Guts filled with fine, unidentifiable particles. A few remains of a small chrysophycean, possibly Uroglena, which was abundant in the water.

9.8.50. Ö Dam, Hilleröd.

Guts mostly empty, such contents as there were mostly fine debris, mainly less than 10.

22.8.50. Arresö

Probably debris and silt less than 5. Also a few minute flagellates and algae, not further identifiable.

Daphnia magna

7.6.50. Bedford College Botany Garden.

Guts black-brown . Almost entirely coarse detritus. The population was not flourishing.

Individuals of this species placed in water from Regent's Park Lake on 8.7.49. consumed and digested some of all the smaller algae, and consumed, without completely digesting such large forms as Phacus and Tribonema.

Daphnia atkinsoni

23.5.50. Berrylands.

Guts green. Gut contents mainly remains of small flagellates and ? Myxophyceae too disintegrated to be identified. Some Ophiocytium and Tribonema; a little detritus.

8.6.50. Witt's Farm, ~~God's Hill~~ Godshill.

Mainly Algae too disintegrated to identify.

Daphnia pulex.

11.8.50. Lynge Dam.

Specimens from here, kept in a dish with algae and detritus, remained in the lighted half of the dish feeding on Euglena and Trachelomonas.

21.10.50. Leg of Mutton Pond, Hampstead Heath. Gut contents mainly black debris, few Algae. The population was not flourishing.

Daphnia obtusa

21.10.49. Bedford College Botany Garden. Guts packed with Trachelomonas and a few other algae.

12.12.49. Bedford College, Botany Garden. Guts greenish yellow. Main contents are: a very small alga, only fragments in faeces; Trachelomonas volvocina, cases in faeces; a round chlorophycean, only seen anteriorly. A medium Cosmarium, a whole colony of Pediastrum boryanum (undigested), and a little detritus were also observed.

16.1.50. Water Lily Pond. Bedford College Botany Garden. Gut-contents mainly coarse debris but some small algae and their remains; Naviculoid Diatom; Trachelomonas volvocina, digested posteriorly and fragments of small filaments.

16.1.50. Pool 2 Bedford College Botany Garden. Mainly coarse detritus. A few algae such as Trachelomonas volvocina, cases only posteriorly, and a large Euglena, not digested.

16.1.50. Pool 5. Bedford College Botany Garden. Mainly algae, some detritus. Scenedesmus, abundant, not digested, Amphora and small Cosmarium, membranes only posteriorly; small Navicula.

1.2.50. Water Lily Pond. Bedford College Botany Garden. Mainly detritus, but many algae, especially Trachelomonas volvocina, and ? xanthophycean.

1.2.50. Pool 5. Bedford College Botany Garden.

Mainly detritus, but fair numbers of algae especially Scenedesmus (not digested); small Cosmarium; and small Navicula.

1.2.50. Pool 7. Bedford College Botany Garden.

Mainly detritus. A few algae such as Scenedesmus (undigested) and fragments of Ulothrix (terminal cells only empty).

15.2.50. Pool 5. Bedford College Botany Garden.

Guts greenish. Mainly detritus but a few small algae as Scenedesmus, not digested; and small Navicula partly digested.

3.50. Pool 4. Bedford College Botany Garden.

Gut contents largely fine detritus, but many small to medium algae and their remains: Scenedesmus, Glenodinium, Cosmarium humile, Cosmarium nr. meneghinii; small diatom, etc.

25.3.50. Pool 3. Epping forest.

Guts bright green. Mainly filled with flagellates and their remains and partially digested narrow filaments of Tribonema.

26.4.50. Water Lily Pond. Bedford College Botany Garden.

Partly fine detritus but mainly algae and their remains, especially large Chlamydomonas, ,few digested; Trachelomonas volvocina, mostly digested posteriorly; Tribonema filaments, partly digested; Chrysococcus, digested posteriorly; small coccoid, digested posteriorly.

26.4.50. Statue Pond. Queen Mary's Garden.

Guts green. Almost entirely filled with algae and their remains, especially very small coccoid, only partially digested; Scenedesmus, not digested; Trachelomonas volvocina, cases only posteriorly; Euglena, undigested; and Amphora, cases only.

5.50. Berrylands.

Guts greenish to black. Mainly detritus but c.33% algae and their remains, especially: *Chrysococcus*, most digested posteriorly; and *Scenedesmus*, little digested; minute naviculoid diatom, mostly digested posteriorly; and minute fragments of *Tribonema*.

7.6.50. Water Lily Pond. Bedford College Botany Garden.

C.70% detritus, remainder largely bacteria; a few algae including a small green form mainly digested posteriorly; *Trachelomonas volvocina*, mostly undigested; *Euglena*, undigested.

7.6.50. Pool 4a, Bedford College Botany Garden.

About half detritus, remainder small algae.

7.6.50. Pool 5. Bedford College Botany Garden.

Mainly debris; very slightly greenish.

8.6.50. Witt's Farm. God's Hill.

Guts more or less packed with algae. More larger forms including *Actinastrum hantzschii*, and *Schroederia setigera*, than in associated *Moina*.

9.7.50. Pool 2. Bedford College Botany Garden.

Mainly small bottom algae; some detritus.

9.7.50. Pool 3. Bedford College Botany Garden.

As in *Daphnia curvirostris* from same pool but slightly higher proportion of bacteria and algae and few filaments.

9.7.50. Pool 4a. Bedford College Botany Garden.

Mainly small bottom algae and filamentous bacteria.

14.10.50. Water Lily Pond. Bedford College Botany Garden.

Fine debris only.

14.10.50. Pool 3. Bedford College Botany Garden.

Guts greenish. Contents a mixture of detritus and small algae.

Daphnia curvirostris.

15.2.50. Pool 4. Bedford College Botany Garden.

Guts green; some very fine detritus but mostly small algae, mainly *Chlamydomonas*, and remains. *Glenodinium* was accumulated in food-groove but not digested.

9.3.50. Pool 4. Bedford College Botany Garden.

Mainly fine detritus but many small to medium algae including: *Scenedesmus*; *Glenodinium*; *Cosmarium humile*; *Cosmarium nr. meneghinii*; small diatom etc.

7.6.50. Pool 4a, Bedford College Botany Garden.

Slightly more detritus than in associated *Daphnia obtuse*, otherwise similar.

9.7.50. Pool 3. Bedford College Botany Garden.

C.50% small algae including *Scenedesmus*, little digested; and *Cymbella* partly digested and 30% moderate detritus to c.30 μ; also bacteria and long fragments filaments and detritus to c.200 μ long and 10 μ to 15 μ thick.

14.10.50. Pools 3 & 4. Bedford College Botany Garden.

Guts filled with a roughly 50-50 mixture of fine detritus and small algae.

Daphnia ambigua

25.10.50. Water Lily Pond. Queen Mary's Garden.

C.60% small algae as: *Chrysococcus*; *Scenedesmus*; and *Chlamydomonas*; all partly digested; also c.40% fine detritus.

Daphnia longispina

24.8.50. Wray Mires.

Food almost entirely remains of very small algae, especially minute *Cosmarium*, digested in part; very small ? diatom fragments; and ? flagellate partly digested.

24.8.50. Wiseen.

Mainly fine detritus. Fragments of a few small algae as <u>Staurastrum ? quadrispinatum</u>.

27.5.50. Viaduct Pond. Hampstead Heath.

Guts green. Contents mainly remains minute algae and bacteria; flagellates; ? Chrysococcus; a few larger forms as small <u>Euglena</u> and small diatom.

14.8.50. Fönstrup Dam.

Almost entirely fine to coarse detritus; much very fine; less than 5μ; but a fair amount 20μ to 30μ; and largest to 40μ .

25.8.50. Deer Paddock. Str̈odam.

Mainly fine detritus, mostly c.5μ to 10μ, but much finer and a fair amount larger to c.40μ, some to c60 . C. 20% small algae especially: <u>Trachelomonas Volvocina</u>, partly digested; <u>Scenedesmus</u>, undigested; <u>Chlamydomonas</u>, partly digested; and small flagellate, some digested.

<u>Daphnia hyalina galeata</u>.

12.8.49. Windermere.

No identifiable algae. Guts of most choked with very fine particles. A little detritus.

24.8.49. Windermere.

Guts green, but contents too fine to be identified, though certainly including fine silt.

<u>Baphnia hyalina s.s.</u>

24.8.49. Loweswater.

Gut contents not identifiable. <u>Coelosphaerium</u> was seen to be rejected repeatedly.

Daphnia hyalina lacustris

14.1.50. Regent's Park Lake.

Guts green, contents very fine; definitely some bacteria, but probably other forms also.

27.8.49. Drunken Duck Tarn, Lake District.

Largely very fine detritus and what looked like fine silt also small algae as: *Trachelomonas*, *Chlamydomonas*, minute *Cosmarium*.

15.6.50. Regent's Park Lake.

Some moderately fine to coarse detritus 10μ to 50μ; but mostly small algae as: *Tetrastrum staurogeniiforme*; very small colonies of *Pediastrum tetras*; flagellates; *Tribonema*, some digested; *Stephanodiscus dubius*, digested posteriorly; *Amphora*, mostly empty; fragments of *Microcystis*; *Chodatella*, mostly digested; and *Achnanthes*.

Daphnia cucullata.

21.7.50. Frederiksborg Slotssö.

Mainly partly digested fragments of *Microcystis* and various larger nannoplankton algae including 'orange' *Scenedesmus* c.20μ; *Chlamydomonas*, partly digested; small colonies of *Sphaerocystis*; Trachelomonas sp. c 30μ, digested.

25.7.50. Frederiksborg Slotssö.

Mainly minute algae; some *Microcystis*.

4.7.50. Highgate 3.

Largely fine debris but many remains of very small algae, mostly unidentifiable. Some were diatomaceous, the largest being c.20μ long. A small palmelloid, and ? *Cyclotella*, membranes only, numerous, also ?

Daphnia Cucullata contd ~~(contd)~~

22.8.50. Arressö.

Mainly remains of very minute algae, largely unidentifiable. Only identifiable fragments were small fragments of Aphanizomanon and odd cells of this, partly digested, but these were few. A small amount of fine detritus, c.5 μ and less.

Ceriodaphnia reticulata

27.8.49. Drunken Duck Pool.

Largely detritus but numerous algae, including Gonatozygon brebisonii, and Achnanthes.

12.10.49. Little Stanmore 2.

Trachelomonas, a few; a few small diatoms; ? bacteria; some detritus.

22.7.50. Teylgaard Sö.

C.70% small algae and 30% fine detritus to 10 μ to 15 μ.

Ceriodaphnia quadrangula

29.7.50. Hjorte Söle.

Guts green; contents very fine, unidentifiable.

3.8.50. Storre Gribsö.

Guts green; contents very fine, unidentifiable.

Ceriodaphnia pulchella

24.8.49. Wray Mires.

Remains of very small algae.

27.8.49. Tarn Hows.

Guts pale green; contents very sparse and fine, unidentifiable.

30.8.49. Windermere.

Guts pale brown. Very fine detritus.

21.7.50. Frederiksborg Slotssö.

Mainly Microcystis, also a few small nanoplankton algae, and a few larger algae. A little detritus.

25.7.50. Frederiksborg Slotssö

Mainly small algae, especially fragments of Microcystis and ? Oocystis

25.7.50 Esrum Sö

Guts bright green. Mainly remains of small algae, but mostly unidentifiable. Some fragments of Tribonema and thecate flagellates.

9.8.50 Ö Dam

Mainly fine detritus to c5 μ to 10 μ ; some remains minute algae.

11.8.50 Bure Sö

Guts green. Contents very fine, unidentifiable.

Ceriodaphnia dubia.

17.9.49. Regent's Park Lake.

Remains of small algae including Trachelomonas, and many unidentifiable.

15.7.50. Regent's Park Lake.

Moderately fine detritus and some small algae including: flagellates; Tribonema; Chodatella sabsalsa etc.,

Ceriodaphnia megalops

27.8.49. Drunken Duck Pool.

Mostly coarse detritus, but numbers of very small algae including Closterium, very small, and Scenedesmus, both only partially digested; also small Navicula, digested.

12.10.49. Little Stanmore 2.

Filled with detritus.

14.8.50. Fönstrup Dam.

Almost entirely detritus of less than 10 μ. A few coarser pieces to c.30 μ.

Simocephalus exspinosus

8'.49. Low Brathsy 3.

Aphanocapsa very abundant anteriorly, none posteriorly; small Amphora cases only posteriorly; Scenedesmus not digested; small Closterium not digested; Ankistrodesmus, partly digested; Chlorococcale, partly digested; Gomphonema, membranes only.

12.8.49. Boat Dock. Low Wray Bay.

Almost entirely algae: Cocconeis, several membranes only; Aphanocapsa anteriorly only; small diatom, membranes only; Staurastrum nr. paradoxum, many membranes, some distorted; small Cosmarium, walls only posteriorly; some Botryococcus; some detritus, fragments of filaments and Cladoceran limbs.

12.8.49. Jetty. Low Wray Bay.

Staurastrum nr. paradoxum, walls only posteriorly; Aphanocapsa, fair quantities; small Nitzschia, a few; Cocconeis, one; Cyclotella; Cosmarium, moderate size, undigested.

12.10.49. Little Stanmore 1.

Guts green; a little detritus; mainly remains of small flagelates and Diatoms.

13.5.50. Highgate 4.

At least 60% small algae and their remains, all at least partly digested, including: Cyclotella; Tribonema; Ophiocytium; small flagellates. Some detritus.

24.6.50. Island Pond. Queen Mary's Garden.

At least 50% small algae, including: Chlamydomonas; Achnanthes; Melosira; Euglena etc.; remainder detritus.

9.8.50. Flats pool Hillerød.

Gut slightly green. Mainly detritus c.2μ to 40μ, mostly c.5 μ to 20μ; a few small algae. Not flourishing.

21.10.50. Leg of Mutton Pond. Hampstead Heath.

Gut green. Mainly detritus; a few small algae; not flourishing.

Simocephalus vetulus

30.8.40. Boathouse. Low Wray Bay.

Gut contents mainly coarse detritus; a few algae as; Botryococcus partly digested; Cocconeis digested; small Navicula, and small Nitzschia, some digested; Staurastrum longispinum, not digested; Palmelloids not digested.

30.8.40 Boat Dock. Low Wray Bay.

Entirely filled with coarse detritus.

12.10.49. Little Stanmore 1.

Gut not green, entirely filled with coarse detritus; very few algae.

12.10.49. Little Stanmore 2.

Filled with coarse detritus.

9.3.50. Hampstead 1.

Almost wholly detritus.

27.5.50. Viaduct Pool. Hampstead Heath.

Almost wholly moderate-sized plant detritus.

9.8.50 Flats Pool. Hilleröd.

Very slight green. Mainly detritus of 2 μ to 40 μ, mostly 5 μ to 20 μ; few small algae. Not flourishing.

Simocephalus serrulatus

29.7.50. Hjorte Söle B.

Guts greenish. Packed with algae and their remains including: Large reguse Cosmarium c.50μ, partly digested; Staurastrum paradoxum, almost all digested; ? Dinastridium, c.50μ without spines, none digested; Oocystis, 20+μ, most at least partly digested; Euastrum eleganc; Asterococcus superbus, scarcely digested; Myxophyceae; ;

Scapholeberis mucronata

25.7.50. Frederiksborg Slotzzöl

C.50% fine and coarse detritus to c.40μ; and c.50% small algae and their remains, especially Microcystis cells.

22.7.50 Teylgaard Sö

Mainly detritus.

25.7.50. Esrum Sö

Guts bright green. Contents very finely divided and not identifiable, save for a few *Achnanthes* cell walls.

29.7.50. Hjorte Söle.

Guts green. Some detritus, but mainly small algae and their remains especially: small green form, mostly digested; medium *Staurastrum*, all empty; *Oocystis*, mostly digested; Peridinium, digested.

10.9.50. Ellesö

Guts green-brown. C.50 - 50 de~~s~~tritus and small algae and their remains.

Moina macrocopa

5.7.50 From Aldwarke Wash, S.Yorkshire.

Individuals of this species put in water from Regent's Park Lake, as *Daphnia* Magna, ingested almost all species of algae present. Digestion was markedly less efficient than in D.magna, the following algae being completely undigested: *Tribonema*; *Cosmarium*; *Chlorobotrys*; *Crucigenia*; *and Scenedesmus*. *Stephanodiscus dubius* was completely digested save for the membranes.

Moina rectirostris

8.6.50 Witt's Farm. God's Hill.

Guts packed with algae; mainly a small green form; also *Scenedesmus*; *Trachelomonas*; small *Pediastrum*; etc.

Bosmina longirostris

30.8.49. Elterwater.

Gut filled with fairly coarse detritus and small algae.

17.10.49. Regent's Park Lake.

Fine detritus and small algae as *Stephanodiscus dubius.*

17.10.49. Children's Boating Lake. Regents Park.

Medium detritus and small algae; at anterior end identifiable in par as *Chlamydomonas* and *Cyclotella*.

10.12.49. Regent's Park Lake.

Guts greenish yellow to brown. Detritus and unidentifiable remains of small algae.

21.12.49. Regent's Park Lake.

Remains of small algae, the largest small specimens of *Stephanodiscus dubius*

22.12.49. Children's Boating Lake. Regent's Park.

Little detritus. Mainly small algae; most important apparently C.B.L. coccoid (a small coccoid alga, probably a species of *Oocystis*, not as yet described, which is very characteristic of this habitat); and *Chodatella*

14.1.50. Regent's Park Lake.

Moderately coarse detritus and unidentifiable small algae.

14.1.50. Children's Boating Lake. Regent's Park.

Very little detritus. Guts packed with small algae, especially: C.B.L. coccoid; and *Chodatella*.

30.2.50. Regent's Park. Children's Boating Lake.

Much as on 14.1.50. but some Tribonema.

15.2.50. Regent's Park Lake.

Mainly detritus; a few small algae.

15.2.50. Children's Boating Lake. Regent'sPark.

Much as on 30.1.50, mostly digested posteriorly.

26.4.50. Water Lily Pond. Queen Mary's Garden.

Fine to moderate detritus; a few unidentifiable small algae.

5.50. Water Lily Pond. Queen Mary's Garden.

Much as on 26.4.50.

15.6.50. Regent'sPark Lake.

About 50% fine detritus, remainder small algae and their remains, mostly digested posteriorly, including: Kirchneriella acuta; flagellates; and filaments of Tribonema, c.4.5 μ broad, and 100 μ long.

4.7.50 Highgate 3.

Moderate to fine detritus to c.12μ ; a few small algae as ? Chrysococcus.

12.10.50 Children's Boating Lake. Regent's Park.

C.10% detritus; remainder small algae and their remains especially: C.B.L. cocoid; Chodatella; , Tetraedron ankistrodesmiformis; and a small flagellate.

Ilyocryptus sordidus

23.1.50 Water Lily Pond. Queen Mary's Garden.

Some-'mud'; many algae, especially Palmelloids.

30.1.50 Children's Boating Lake. Regent's Park.

Mainly small palmelloid algae.

15.6.50. Regent's Park Lake.

Almost packed with small algae and their remains especially: Achnanthes; Tetraedron minimum; Chodatella; Tribonema; and Palmelloids.

6.50. Water Lily Pond Queen Mary's Garden.

Guts packed with small algae and their remains, mainly palmelloids.

12.10.50 Children's Boating Lake. Regent's Park.

Contents almost entirely small algae especially C.B.L. coccoid, membranes only posteriorly.

Macrothrix laticornis

9.3.50 Hampstead 3.

Some detritus; mainly remains of very small algae including: Cyclotella, and Amphora.

Lathonura rectirostris

17.8.49 Brother's Water.

A little detritus but mainly algae, including: large numbers of Cymbella and Eunotia; small numbers of a medium Cosmarium. All membranes only posteriorly.

Streblocerus serricaudatus

27.8.49. Drunken Duck Pool.

Moderately fine detritus.

Acantholeberis curvirostris

29.7.50. Hjorte Söle B.

Mainly fine detritus; a few small algae, mostly Myxophyceae.

3.8.50 Bönderness Mose.

Small bottom algae in proportions exactly as those in habitat.

25.8.50. Hjorte Söle A.

C.50% small algae as Oocystis, partly digested; and some Botryococcus; c.50% detritus.

Macrothrix
~~Echinisca~~ tenuicornis

Godshill
8.6.50 Witt's Farm. ~~God's Hill~~.

Guts packed with small algae as Trachelomonas; small green coccoid etc; very little detritus.

Eurycercus lamellatus

12.8.49. Boat Dock. Low Wray Bay.

Very much detritus and plant fragments; limbs of Cladocera etc. algae scarce including: Staurastrum, membranes only; Navicula and Cocconeis membranes only; Scenedesmus and palmelloids, some, at least, undigested.

12.8.49. Jetty. Low Wray Bay.

Almost entirely detritus and plant fragments; scarcely any algae; a few fragments of filaments; and some *Aphanocapsa*.

27.8.49. Drunken Duck Tarn. Lake District.

Mainly detritus, plant fragments, fragments of algal filaments etc. Some *Botryococcus* , undigested; *Cyclotella* membranes; and small green form, apparently digested.

30.8.49. Boat House. Low Wray Bay.

Entirely coarse detritus.

Acroperus harpae

19.8.49. Blelham Tarn.

Mainly coarse detritus.

13.5.50. Highgate 4.

Almost entirely detritus; a few palmelloids.

Alonopsis elongata

11.8.50. Bure Sö.

Entirely filled coarse detritus.

Graptoleberis testudinaria

14.8.50. Lille Fönstrup Dam.

Fine to moderately fine detritus; much less than 5μ; some to 10μ½

Leydigia Leydigi

22.12.49. Children's Boating Lake. Regent's Park.

C.50 - 50 C.B.L. coccoid and fine detritus.

14.1.50. Children's Boating Lake. Regent's Park.

C.50 - 50 detritus and algae, especially C.B.L. coccoid, not well digested.

30.1.50 Children's Boating Lake. Regent'sPark.

Mainly detritus; a fair amount of algae especially C.B.L. coccoid.

15.2.50. Children's Boating Lake. Regent's Park.

Mainly detritus; c.20% algae, especially Chodatella.

24.4.50. Regent's Park Lake.

Fairly coarse detritus; a few small algae.

15.6.50. Regent'sPark Lake.

Fine to coarse detritus; mostly c.5μ to 10μ; some to 30μ. A few small algae.

6.50. Water Lily Pool. Queen Mary's Garden.

Mainly detritus.

Alona affinis.

18.8.49. Blelham Tarn.

Mainly fine detritus; a few small algae; largest a medium Cosmarium.

19.8.49. Blelham Tarn

Fine detritus.

27.8.49. Drunken Duck Tarn. Lake District.

Fairly coarse detritus; scarcely any algae.

14.1.50. Regent's Park Lake.

Moderately fine detritus; no algae.

9.3.50. Hampstead 2.

Mainly fine detritus; a few small algae.

13.5.50 Highgate 2.

C.70% detritus and 30% algae including: Cyclotella, all digested posteriorly; and small, and medium Cosmarium, few digested.

15.6.50. Regent's Park Lake.

Mainly fine detritus; c.30% small algae as : Achnanthes; and Tetraedron minimum.

14.8.50. Esrum Sö.

Mainly very fine detritus; few algae.

Alona rectangula

13.5.50. Highgate 2.

Mainly Cyclotella and Achnanthes.

Rhynchalonella rostrata

13.5.50. Highgate 2.

Mainly detritus. Some Cyclotella and Achnanthes ; but these mostly undigested.

Alonella excisa.

19.8.49. Blelham Tarn.

Mainly rather coarse detritus; a few small algae.

Alonella nana

27.8.49. Drunken Duck Pool. Lake District.

Fine detritus.

Pleuroxus truncatus

25.7.50. Frederiksborg Slotssö

Mainly small algae; a large Trachelomonas hirsuta, scarcely digested, was largest form present. Otherwise species taken were much the same as those taken by Sida crystallina, but digestion seemed to be less efficient.

27.5.50. Viaduct Pond. Hampstead Heath.

Mainly small algae.

Pleuroxus uncinatus

13.5.50. Highgate 4.

Mainly detritus; a few algae as Trachelomonas and palmelloids

Chydorus sphaericus

16.8.49. Codale Tarn.

Gut contents algae and detritus fragments of considerable size.

22.12.49. Children's Boating Lake. Regent's Park.

Mainly small algae; chiefly C.B.L. coccoid; digestion less efficient than in Bosmina

14.1.50. Children's Boating Lake. Regent's Park.

Guts packed some detritus and C.B.L. coccoid, undigested, even posteriorly.

14.1.50. Regent's Park Lake.

Mainly detritus; a few , bacteria.

16.1.50. Pool 3. Bedford College Botany Garden.

Moderate to fine detritus; a few small algae too disintegrated to identify.

15.2.50. Children's Boating Lake. Regent's Park.

Some detritus but mainly algae, especially C.B.L. coccoid and Chodatella.

15.2.50. Bedford College Botany Garden.

Mainly fine to moderately fine detritus. Afew small algae.

9.3.50 Hampstead 1.

Mainly detritus; some small algae.

9.3.50. Hampstead 2.

Mainly fine detritus.

25.3.50. Forest Hotel. Epping Forest.

Mainly detritus; also small coccoids and their remains; and Peridinium.

25.3.50. Connaught Water.

C.50 - 50 detritus and small algae as Trachelomonas and other small flagellates and their remains.

13.5.50. Highgate 2.

Mainly Cyclotella and other small diatoms, which were partly digested; also much detritus.

15.6.50. Regent's Park Lake.

Largely detritus; a few small algae as Scenedesmus; and small coccoids.

29.7.50. Hjorte Söle B.

C50 - 50 detritus and small algae.

Polyphemus pediculus

21.7.50. Frederiksborg Slotssö

Coarse vegetable detritus, to over 40μ .

25.7.50. Esrum Sö.

Mainly fine vegetable detritus.

These are the only two examinations of the food of this species which I have performed. Whenever I have seen this species the gut contents have appeared to be brown and given the impression of consisting of vegetable detritus.

Latona setifera

27.8.49. Tarn Hows.

Almost entirely coarse detritus.

Ceriodaphnia laticaudata

9.8.50. Flats Pool. Hillerőd.

Fine to medium detritus but mostly less than 10μ.

Pleuroxus laevis

9.8.50. Flats Pool. Hillerőd.

Detritus mostly c.10μ.

Appendix 2

Association of Daphnia cucullata, with nannoplankton algae.

13.5.50. Highgate 3.

Very numerous, eggs c.15 .

Algae very abundant, mostly small, detritus moderately abundant.

The principal algae in order of abundance were: Cyclotella app., c.8 μ to 15 μ Kephyrion sp. ; Tetrastrum staurogeniiforme ; very small Cosmarium; colonial Dinobryon; Aphanocapsa; Uroglena; Mallomonas; solitary Dinobryon; Trachelomonas volvocina; Lagerheimia wratislawensis; small Navicula; Euglena; Scenedesmus.

5.7.50. Highgate 3.

Very scarce, eggs c.5.

53.9% of seston consists of detritus. 76.49% of remainder consists of Myxophyceae, mainly Aphanocapsa. Remaining algae all rather scarce, in order of abundance: Chromulina, 4.6%; ? Dysmorpococcus, 3.0%; Kirchneriella, 1.8%; Chroomonas acutus, 2.0% ; Schroeteria setigera, 1.4%; Tetrastrum staurogeniiforme, .8%; Cyclotella, .8%; Stephanopyxis moniliforme, .6%; and Ochromonas, .4%. Other Algae mostly of small size accounted for 8.2%

21.7.50. Frederiksborg Slotzzo"

Numerous, eggs c.3.

Microcystis extremely abundant. There were other smaller algae , some of which may have been abundant; but it was impossible to estimate these, since they were so overshadowed by the Microcystis water-bloom.

5.8.50. Ager Sö

Detritus moderate; bacteria fairly abundant; algae very abundant.

The principal algae in order of abundance were: Anabaena spiroides; Staurastrum gracile; small Cryptomonas; Chlamydomonas; Pyramimonas; other small flagellates; and Coelosphaerium.

22.8.50. Arresső.

Very numerous, eggs c. .9 (0 to 2).

? Bacteria abundant; detritus and algae fairly abundant.

Principal algae in order of abundance were *Lyngbya*; *Gomphosphaerium*; *Scenedesmus* spp.; *Synechocystis*; *Aphanocapsa*; *Anabaena*; *Chodatella*; *subsalsa*; *Elakatothrix gelatinosa*; *Microcystis* spp.; *Chroococcus limneticus*; *Tribonema*; *Chlamydomonas*; small *Cosmarium*.

11.9.50. AlmindSő.

Probably abundant, since some were taken in very shallow water. Algae moderately abundant, little detritus. It was not possible to examine the nannoplankton algae. The dominant forms in the net-algae were *Melosira granulata*; and *Tabellaria fenestrata v. asterionelloides*. There were no *Myxophyceae*.

11.9.50. UglSő.

Not very numerous.

The water was coloured yellow-green by the abundant algae. It was not possible to examine these thoroughly but the principal were: *Uroglena*; *Botryococcus*; *Cyclotella* spp. ; and other flagellates. I *Myxophyceae*.

Appendix 3.

Algae and Cladocera records for a pool (the Water Lily Pond) in Bedford College Botany Garden.

22.11.49.

Daphnia obtusa, very numerous eggs almost nil.

Detritus moderate; algae sparse. Principal were: Trachelomonas volvocina; large Chlamydomonas; and ? Gymnodinium .
There were also some Bacteria and Ciliates.

12.12.49.

Daphnia obtusa, very numerous, eggs c.7.5. (0 to 12)
Algae abundant. Principal were Chlamydomonas; Trachelomonas volvocina; ? Monas; Cryptomonas; and Euglena.

16.1.50.

Daphnia obtusa, abundant, eggs 3.7 (0 to 10).

Total seston. 4ml. per litre, of which algae etc. accounted for 60%; Principal living forms were: Filamentous Bacteria, 86.8%; colourless flagellates 2.8%; small coccoids 3.0%; other Bacteria 1.9%; Chromulina 1.6%; and ; Ciliates, 1.26%;

Daphnia obtusa, very abundant, eggs 6 (0 to 11). Chydorus sphaericus,

Total seston c.2 ml per litre. detritus was 65.28%. Living forms consisted almost entirely of bacteria, 91.4%.

15.2.50.

Daphnia obtusa, abundant, eggs 6.2 (0 to 10).

Total seston c. . 2ml. per litre. Detritus constitutes 47.1%. Of the remainder 95.8% was bacteria; the remainder small flagellates.

10.3.50.

Daphnia obtusa, abundant eggs 6.6 (0 to 15).

Total seston c. .2ml. per litre. detritus 53.2%. 64.6% of the remainder consisted of bacteria, the rest of small algae and flagellates of which the following were the most abundant: Cryptomonas, 25.2%; Scenedesmus, 2.4%; and Chlamydomonas, 1.3%.

25.4.50.

Daphnia obtusa, abundant eggs 7.6 (6 to 9).

Total seston c..1ml. per litre. Of this 43.0% was detritus. Of the remainder 43.2% was bacteria, the rest algae and flagellates, of which the principal were: Cryptomonas, 27.6%; Scenedesmus obliquus, 7.8%; Trachelomonas volvocina, 6.8%; and Nitszchia acicularis, 5.2%.

7.6.50.

Daphnia obtusa, abundant, eggs c. 1.0 in parthenogenetic individuals but c.70% were ephippiate.

Total seston less than .1 ml per litre. Of this 66.5% was detritus. Of the remainder 75% was bacteria, the rest consisting of various algae of which only Chlamydomonas, 4.6%, was at all frequent.

10.7.50.

Daphnia obtusa, very abundant, eggs very low, 0.6 (0 to 2).

Owing to lemna cover etc. it was impossible to obtain a good water sample. Detritus appeared to be abundant there were virtually no algae.

8.8.50.

Daphnia obtusa, very abundant.

Daphnia curvirostris, very numerous.

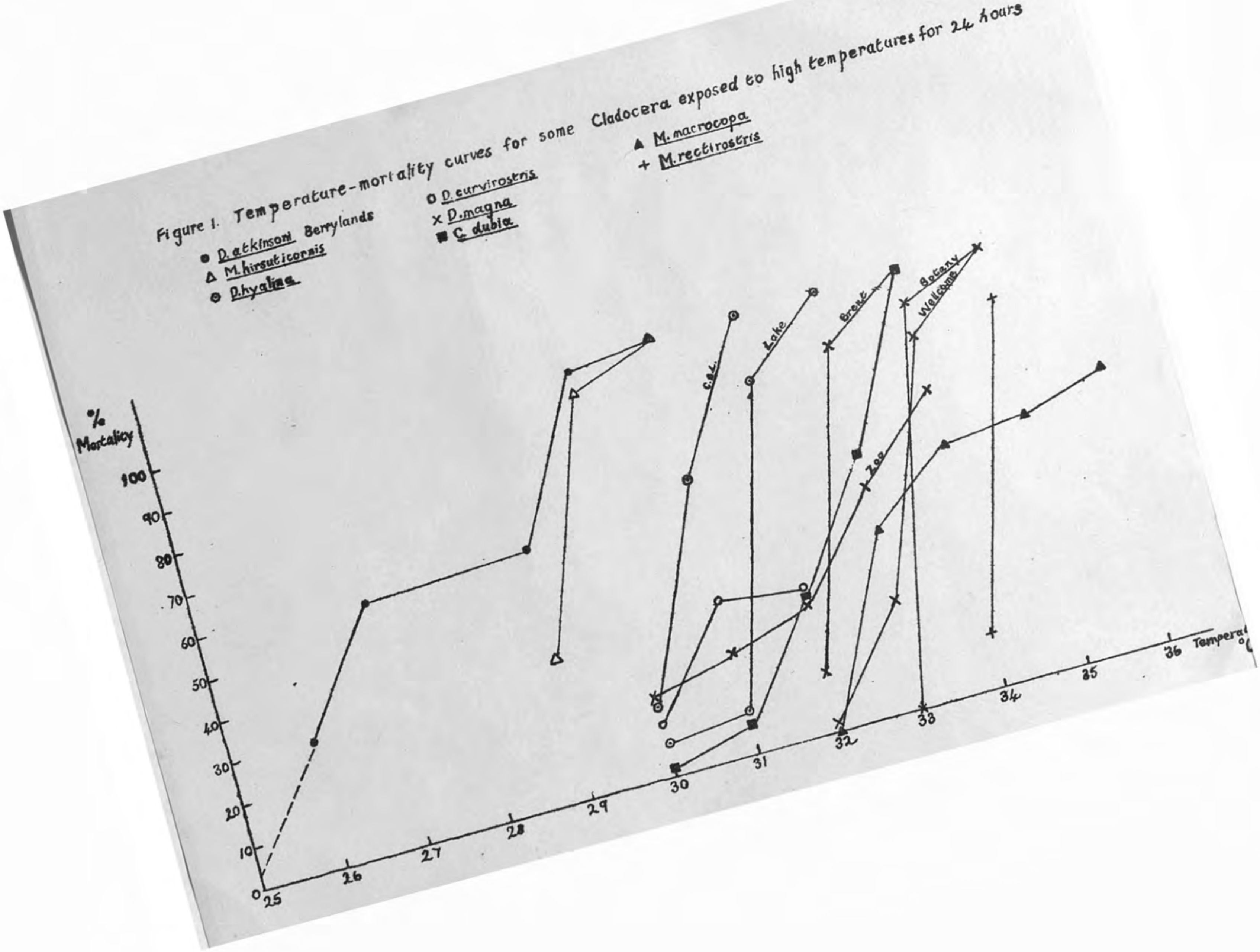
Total seston .3 ml. per litre, of which c.62% was detritus. Of the remainder bacteria comprised 73.1%; The other principal constituents were: colourless flagellates 7.7%; small coccoids, 6.4%; filamentous bacteria 6.4%; and small flagellates 2.6%.

14.10.50.

Daphnia obtusa, not very numerous, eggs 3.0 (2. to 4).

Daphnia curvirostris, abundant, c.70% ephippiate, eggs c.4 (3 to 6). Total seston c. .6 ml. per litre, of which over 80% was detritus; of the remainder over 99% was bacteria.

Figure 1. Temperature-mortality curves for some Cladocera exposed to high temperatures for 24 hours



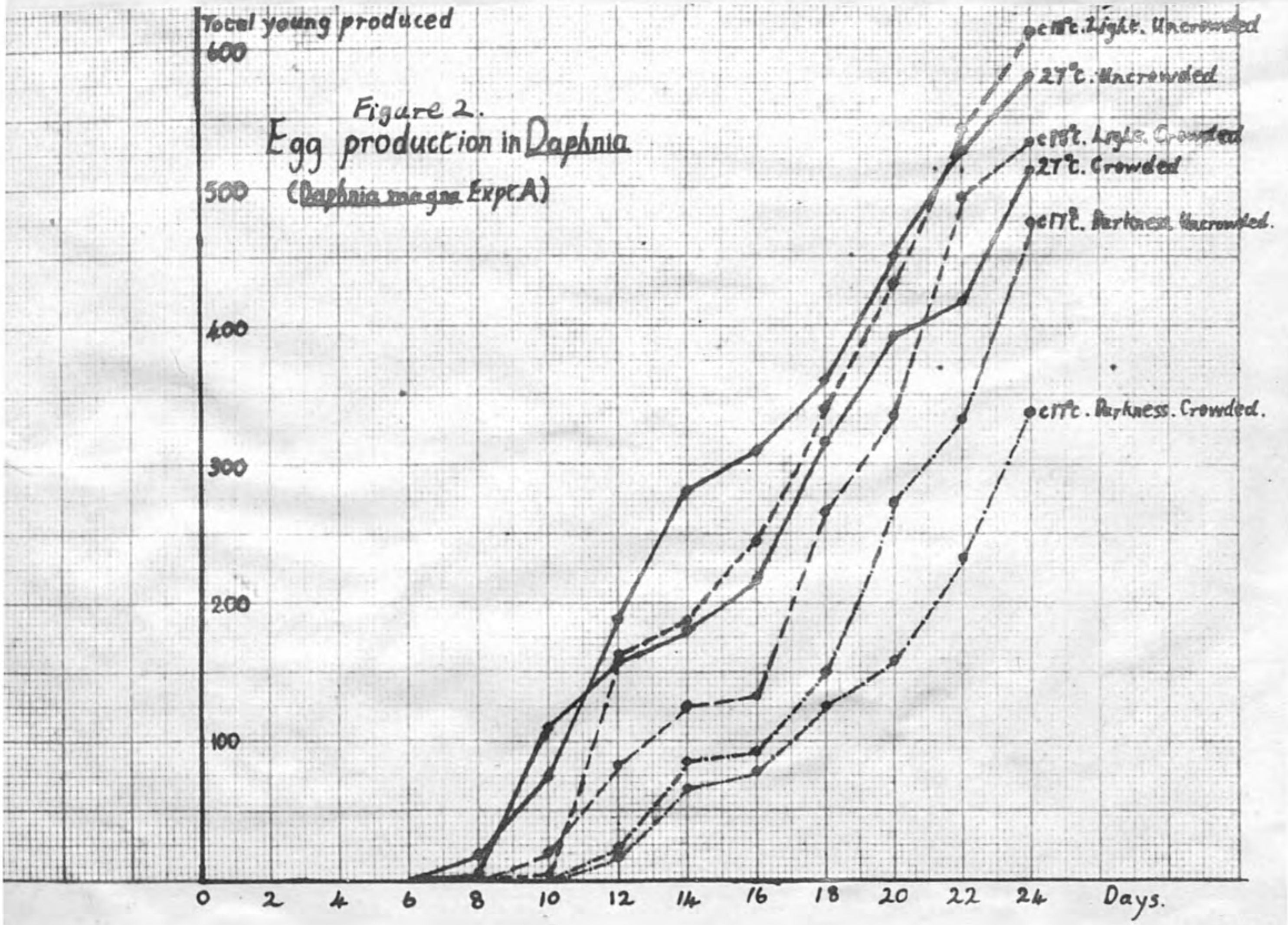


Figure 2.
Egg production in Daphnia
(Daphnia magna Expt A)

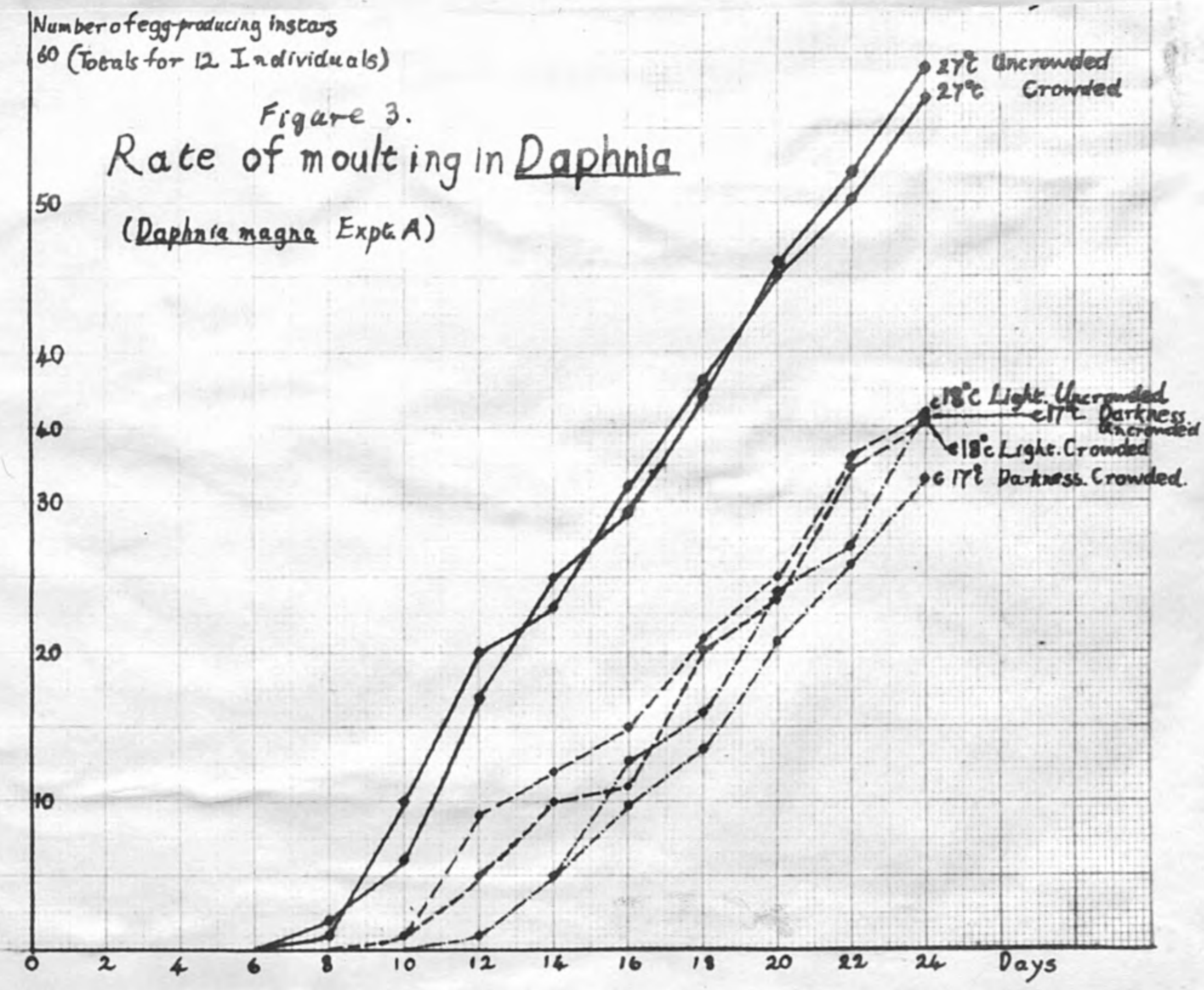
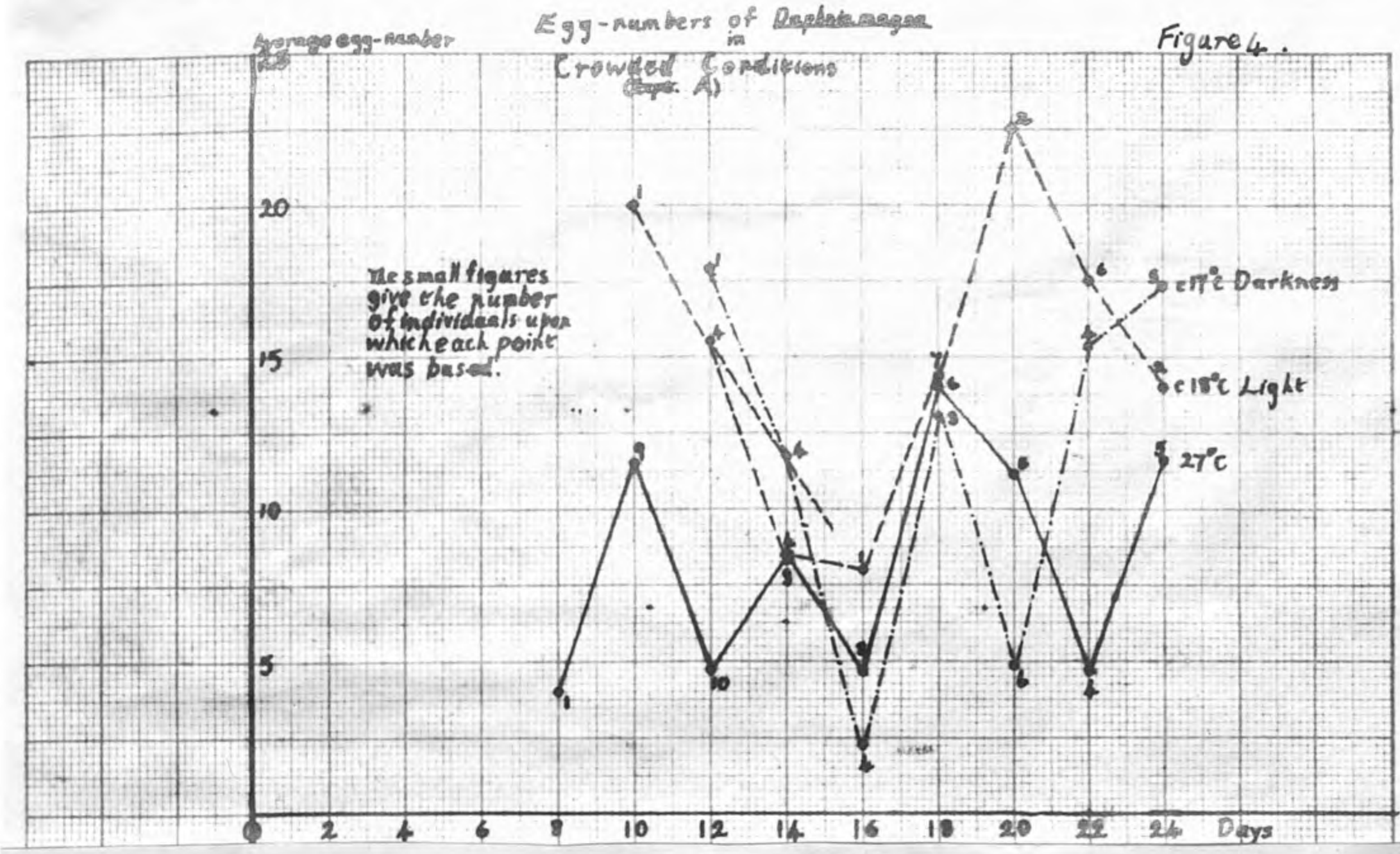


Figure 3.
Rate of moulting in *Daphnia*

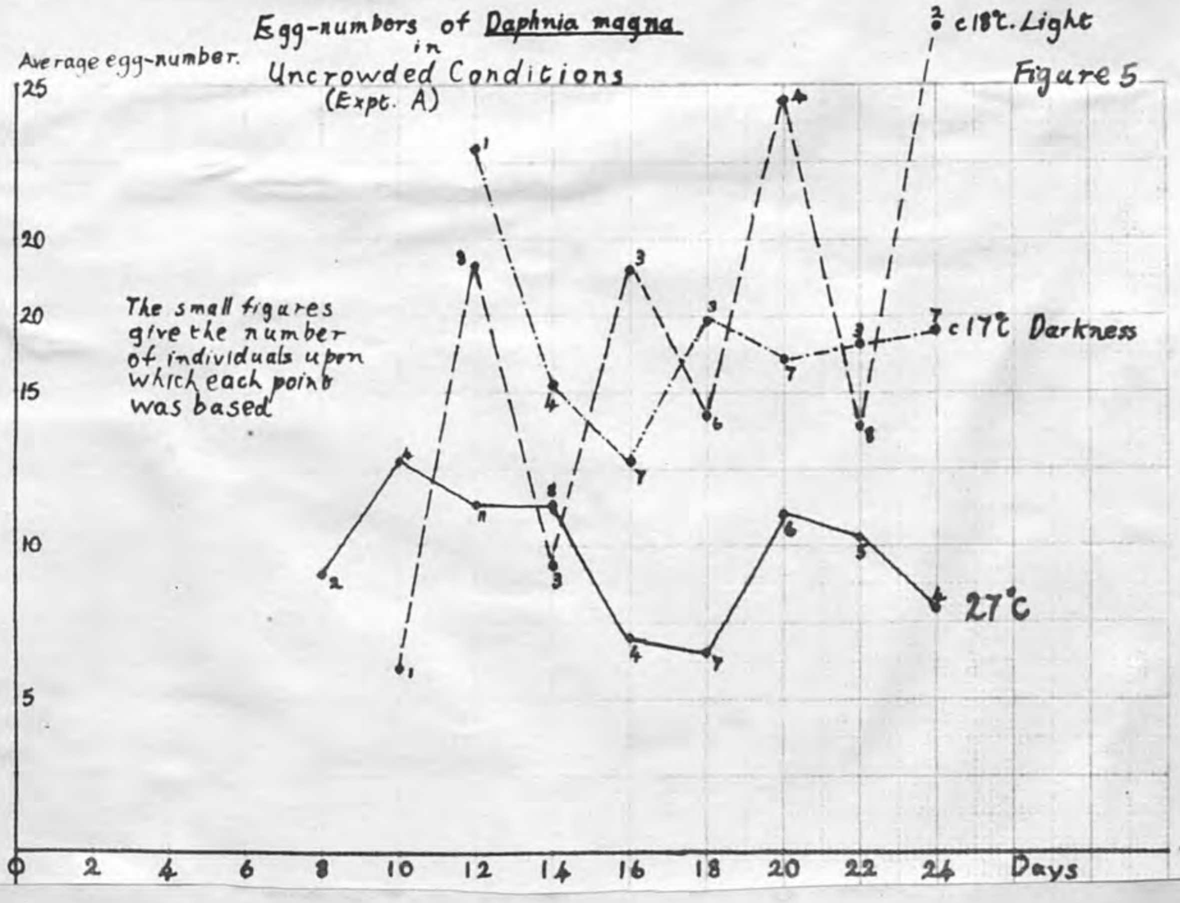
(*Daphnia magna* Expt. A)



Egg-numbers of *Daphnia magna* in Crowded Conditions (Expt. A)

Figure 4.

The small figures give the number of individuals upon which each point was based.

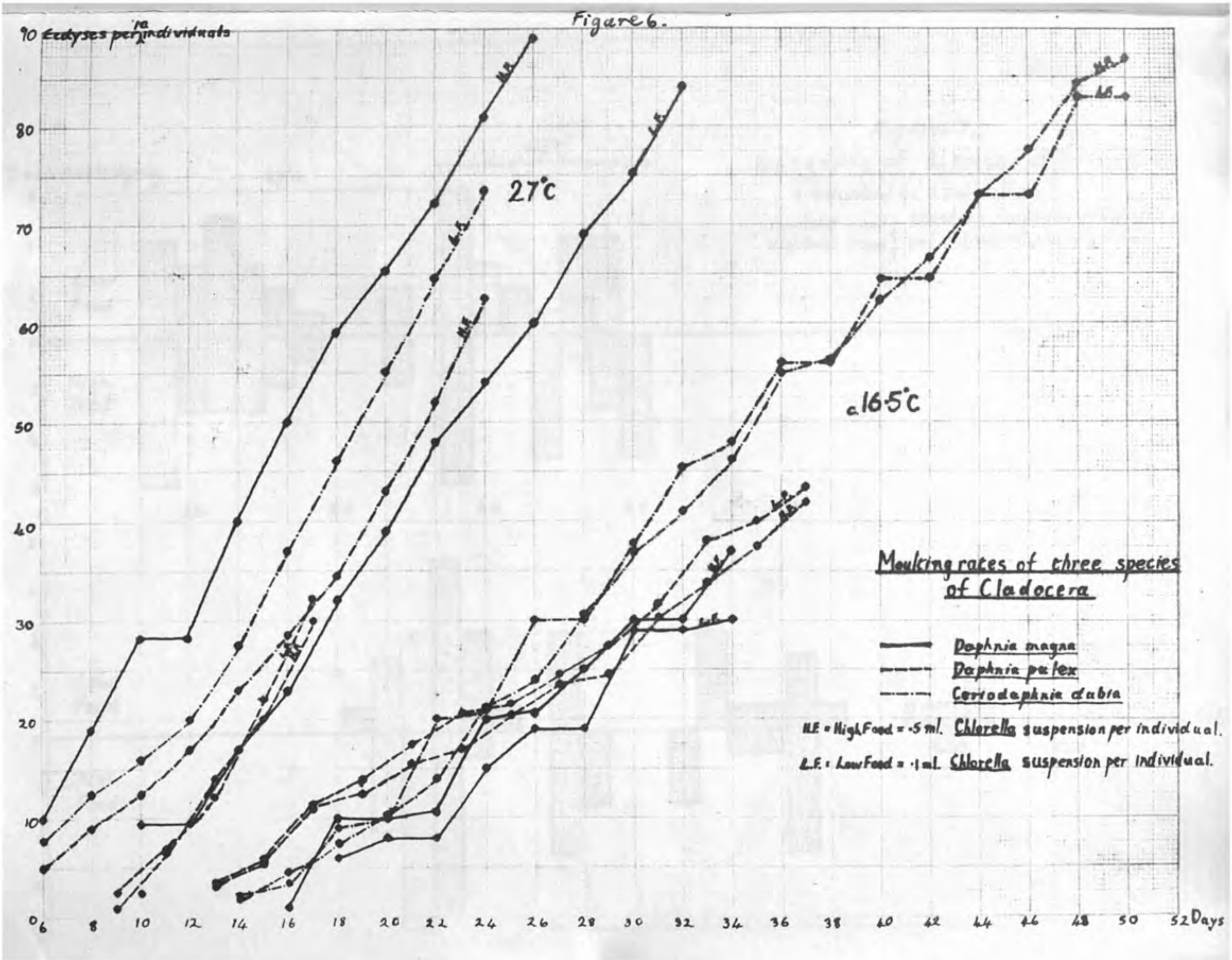


Egg-numbers of *Daphnia magna* in Uncrowded Conditions (Expt. A)

Figure 5

The small figures give the number of individuals upon which each point was based

Figure 6.


90 Ecdyses per 10 individuals
80
70
60
50
40
30
20
10
0
6
8
10
12
14
16
18
20
22
24
26
28
30
32
34
36
38
40
42
44
46
48
50
52 Days
27°C
c16·5°C
H.F.
L.F.
Moulting rates of three species of Cladocera
Daphnia magna
Daphnia pulex
Ceriodaphnia dubia
H.F. = High Food = ·5 ml. Chlorella suspension per individual.
L.F. = Low Food = ·1 ml. Chlorella suspension per individual.

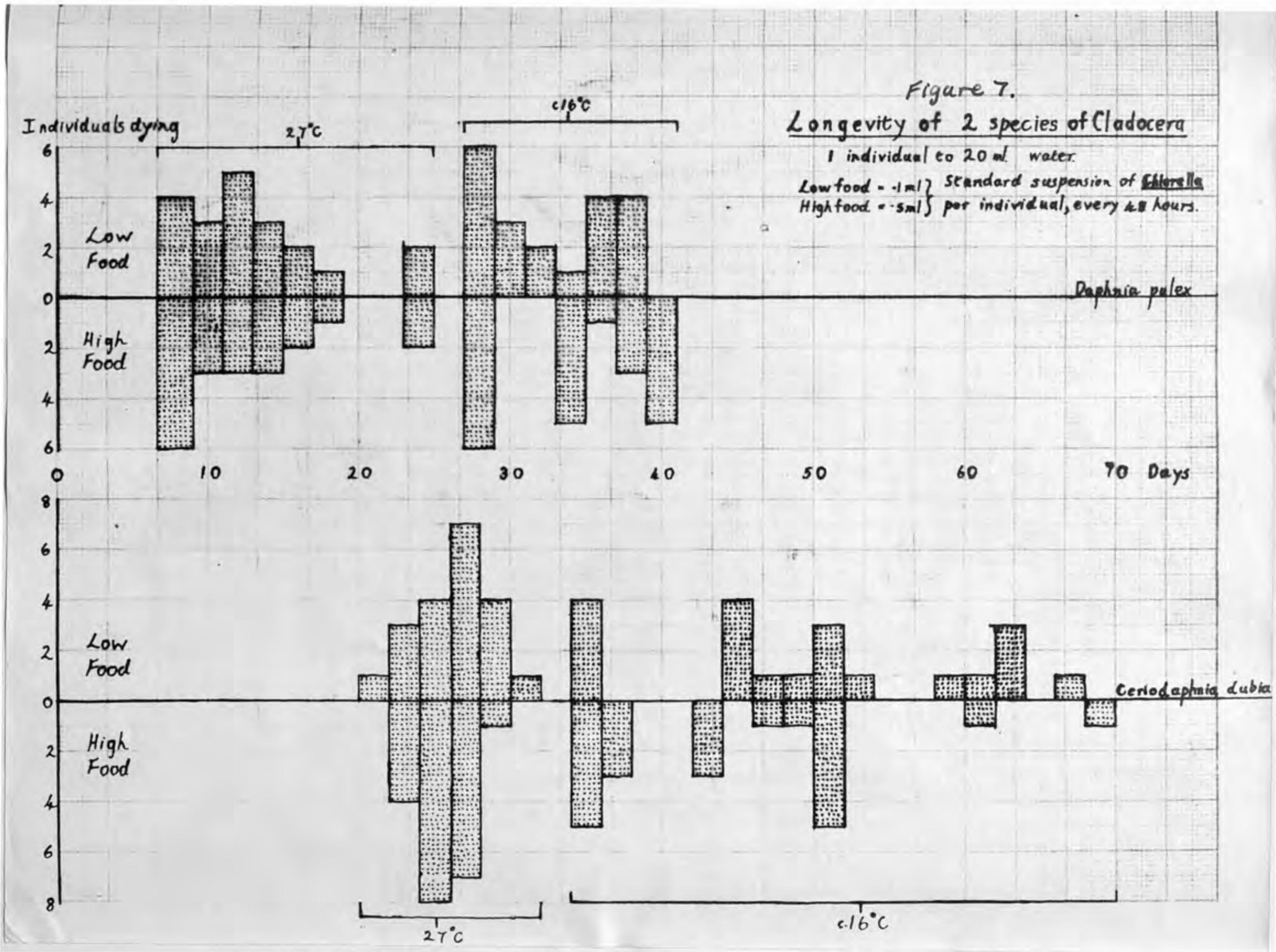


Figure 7.

Longevity of 2 species of Cladocera

1 individual to 20 ml. water.

Low food = ·1 ml } Standard suspension of *Chlorella*
High food = ·5 ml } per individual, every 48 hours.

Table I: Sizes, and egg-numbers of individuals from populations of *Daphnia* kept in various culture conditions.

Species:	Daphnia obtusa (Stable populations)				Daphnia magna (Sparse cultures)	
Culture:	Soya-soil		Yeast-Alga		Alga	
	Size(mm)†	Egg-number	Size(mm)†	Egg-number	Size(mm)†	Egg-number
	1·45	0	1·50	0	2·45	0
	1·48	4	1·50	3	2·70	16
	1·50	0	1·55	0	2·75	10
	1·53	0	1·55	4	2·75	0
	1·70	2	1·55	4	2·83	16
	1·70	0	1·58	0	2·88	16
	1·75	4	1·70	13	2·88	19
	1·78	1	1·85	6	2·90	24
	1·78	0	1·90	5	2·93	10
	1·80	0	1·90	8	3·05	15
	1·85	0	1·93	7	3·25	20
	1·90	0	2·00	13	3·40	15
	1·93	2	2·00	8	3·40	20
	1·98	0	2·00	0	3·63	37
	2·03	0	2·50	21	3·70	0
	2·05	0	2·55	9	3·80	14
	2·08	0	2·70	8	3·99	27
	2·13	0			4·05	15
	2·23	0			4·05	32
					4·50	7
					4·55	27
					4·60	35
Means	1·84±·05*	·65±·29*	1·90±·09*	6·41±·33*	3·38±·11*	17·05±·95*

* Standard Error

† Length measured frons to base of carapace spine.

Table 2. Mortality of *Cladocera* exposed to high temperatures for 24 hrs.

Species	Source	Temperature °C	Number used	% Mortality
Daphnia magna	Gull Pond, Zoo	30	50	20
		30	50	18
		31	50	24
		31	50	24
		32	50	30
		33	15	53
		34	14	71
Daphnia magna	Brent	32	25	34
		32	75	12
		32	50	10
		32	50	0
		33	50	82
		33	50	91
		34	50	100
		35	50	100
Daphnia magna	Wellcome Institute	32	50	0
		32	50	4
		33	50	12
		33	50	40
		34	50	84
		35	50	100
Daphnia magna	Botany Garden	33	25	0
		34	50	84
		34	25	100
		35	15	100
Daphnia atkinsoni	Berrylands	26	50	30
		27	50	60
		27	50	56
		29	20	60
		30	50	100
		30	49	93.9
		33	25	100
Daphnia atkinsoni	Witt's Farm	27	25	8
		32	25	12
		32	24	25
		33	25	40
		34	25	80
		34	25	100
		35	20	95
		35	25	96
Daphnia pulex	Brent	34	50	100
Daphnia pulex	Leg of Mutton	30	25	40
		30	50	44
		32	50	100

Table 2. (Continued)

Species	Source	Temperature °C	Number used	% Mortality
Daphnia pulex	Botany Garden	27	25	0
		27	25	0
		32	40	12·5
		33	50	74
		33	50	80
		34	50	100
		34	50	100
Daphnia curvirostris	Gull Pond, Zoo	30	50	8
		30	50	18
		31	22	44
		31	50	32
		32	50	30
		32	50	38
Daphnia curvirostris	Aldwarke	33	50	100
Daphnia obtusa	Queen Mary's Garden Autumn.	30	50	6
		30	50	4
		31	50	18
		31	50	16
		32	50	10
		32	50	16
		33	50	26
		33	50	68
		34	50	70
		34	50	92
Daphnia obtusa	Queen Mary's Garden Summer	32	50	6
		32	50	2
		33	15	100
Daphnia obtusa	Witt's Farm	34	25	80
		35	20	95
		35	25	96
Daphnia obtusa	Botany Garden	27	25	0
		32	50	30
		33	50	26
		33	50	20
		33	50	72
		34	25	100
		34	25	96
		34	50	100
		34	25	100
Daphnia hyalina	Regent's Park Lake	30	50	8
		31	20	10
		32	50	56
		32	25	96
		32	25	100
		33	50	100
		33	50	100

Table 2. (Continued)

Species	Source	Temperature °C.	Number Used	% Mortality
Daphnia hyalina	Children's Boating Lake	30	50	22
		30	50	12
		31	50	72
		31	50	60
		32	50	100
		32	50	100
		33	50	100
Ceriodaphnia pulchella	Queen Mary's Garden	32	50	6
		33	40	57·5
		34	50	100
Ceriodaphnia dubia	Regent's Park Lake	30	25	8
		30	25	4
		31	50	4
		31	25	12
		32	50	18
		32	50	46
		33	50	56
		33	50	66
		34	25	100
Moina rectirostris	Witt's Farm	34	15	13·3
		35	15	86·7
		35	50	90
Moina macrocopa	Aldwarke	32	50	0
		32	50	0
		33	50	40
		33	50	4
		33	50	76
		33	50	50
		34	50	68
		35	50	70
		36	20	76
		37	25	100
Macrothrix hirsuticornis	~~God's Hill~~ Godshill	29	40	40
		29	50	28
		30	50	92
		31	50	100
		32	50	100
		33	50	100

Table 3. L.T.50's of various Cladocera (24 hours exposure)

Species	Source	L.T.50 (°C)	Expected. Thermal Resistance
Moina rectirostris	God's Hill,** Hants.	c.34·5°C *	very high.
Daphnia obtusa	God's Hill,** Hants.	c. 33·8 *	high.
〃 magna	College Botany Gd.	c 33·5 *	high.
〃 〃	Wellcome Institute	33·4 ± ·2	high.
Moina macrocopa	Aldwarke Wash.	c. 33·3 *	very high.
Daphnia magna	Zoo	c 33 *	high
〃 obtusa	Q. M. G., Autumn	33·0 ± ·2	high
〃 〃	College Botany Gd.	32·9 ± ·3	high
〃 atkinsoni	God's Hill, Hants.	32·9 ± ·2	very high
Ceriodaphnia pulchella	Q. M. G.	32·9 ± ·1	low
Daphnia pulex	College Botany Gd.	32·6 ± ·1	moderately high.
〃 magna	Brent	32·5 ± ·1	high.
〃 obtusa	Q. M. G., Summer.	c. 32·5 *	high.
Ceriodaphnia dubia	Regent's Park Lake	c 32·3 *	moderate
Daphnia hyalina	Regent's Park Lake	31·6 ± ·3	low
〃 hyalina	C. B. L.	30·8 ± ·1	low
〃 pulex	Leg of Mutton Pond	30+ *	moderately high
Macrothrix hirsuticornis	God's Hill **	29·1 ± ·3	low
Daphnia atkinsoni	Berrylands	c 26·8 *	very high

Abbreviations:-

L.T.50 = temperature for 50% mortality.

* figures by direct interpolation.

College Botany Gd. = Bedford College Botany Garden.

Zoo = The Gull Pond, Zoological Gardens, Regent's Park.

Q. M. G. = Statue Pond, Queen Mary's Garden, Regent's Park.

C. B. L. = Children's Boating Lake, Regent's Park.

** Correct spelling = Godshill

Table 4. Experiment A. Reproduction in Daphnia magna. Experimental data.

Days	27°C					18°C Room A					17°C Room B				
	Uncrowded				Crowded	Uncrowded				Crowded	Uncrowded				Crowded
8	0/0	7/1	11/1	0/0	4/1	—	—	—	—	—	—	—	—	—	—
10	19/1	16/1	14/1	7/1	105/9	0/0	0/0	6/1	0/0	20/1	—	—	—	—	—
12	36/2	29/3	32/3	27/3	47/10	36/2	50/3	1/0	67/3	62/4	0/0	0/0	23/1	0/0	18/1
14	24/3^{D}	19/1	19/2	29/2	25/3	8/1	0/0	19/2	0/0	42/5^{D}	24/1^{D}	20/1	2/1	15/1	47/4^{LL}
16	0/1	8/1	8/1	12/1	37/8^{DD}	0/0	20/1	14/1	23/1	8/1^{DD}	22/1	5/2	27/2	35/2	10/4
18	0/0^{D}	9/2^{D}	9/2	28/3	34/6^{D}	41/2	28/2	18/2	8/0	101/7^{D}	0/0	18/1	14/1	20/1	39/3
20	—^{L}	24/2	16/2	26/2	56/5	0/0	18/1	22/1	50/2	45/2	44/2	25/2	20/1^{D}	24/2	29/6
22	—	21/1	22/2	8/1^{D}	19/4^{DD}	48/3	23/2	30/2	12/1	105/6	0/0	16/1	15/1	19/1	61/4
24	—	21/1	1/1	10/2	57/5^{DD}	—^{LL}	21/1	0/0	32/1	28/2	40/2	37/2	13/1	29/2	87/5
Totals	79/7	154/13	132/15	147/15	434/51	133/8	160/10	110/9	192/8	411/28	130/6	121/9	114/8	142/9	291/27
	512/50					595/35					507/32				

D = 1 dead L = 1 lost or accidentally killed.

Explanation:- In this table and table 8 the upper figure of each fraction represents the number of living young observed; the lower figure represents the number of adult exuviae.

Table 6. Experiment A. *Daphnia magna* Total ecdyses produced per 12 adult individuals

	27°C		18°C Room A		17°C Room B	
Days	Uncrowded	Crowded	Uncrowded	Crowded	Uncrowded	Crowded
8	2	1	0	0	0	0
10	6	10	1	1	0	0
12	17	20	9	5	1	1
14	25	23	12	10	5	5
16	29.4	31	15	11.1	12.6	9.8
18	37.0	38.2	21	20.4	15.9	13.4
20	46.0	44.9	25	23.4	23.6	20.6
22	52.0	50.2	33	32.4	27.2	25.4
24	58.9	57.1	36	35.4	35.6	31.4

Table 5. Experiment A. *Daphnia magna*. Total young produced per 12 individuals

	27°C		18°C Room A		17°C Room B	
Days	Uncrowded	Crowded	Uncrowded	Crowded	Uncrowded	Crowded
8	18	4	0	0	0	0
10	74	109	6	20	0	0
12	188	156	160	82	23	18
14	279	181	187	124	84	65
16	309.6	218	244	132.7	93.1	77
18	359.7	318.8	339	267.4	149.8	123.8
20	448.7	393.5	429	334.9	273.1	158.6
22	525.2	418.8	542.0	492.4	333.1	231.8
24	580.1	513.1	612.7	534.4	475.9	336.2

Table 7. Experiment A. *Daphnia magna*. Average egg-numbers.

	27°C		18°C Room A		17°C Room B	
Days	Uncrowded	Crowded	Uncrowded	Crowded	Uncrowded	Crowded
8	9	4	—	—	—	—
10	14	11.7	6	20	—	—
12	11.3	4.7	19.1	15.5	23	18
14	11.4	8.3	9.3	8.4	15.3	11.8
16	7.0	4.6	19.0	8.0	12.8	2.3
18	6.6	14.0	14.5	14.4	17.3	13.0
20	11.0	11.2	24.5	22.5	16.1	4.8
22	10.2	4.8	14.1	17.5	16.7	15.3
24	8.0	11.4	26.5	14.0	17.0	17.4
Means	10.2	8.5	17.0	14.7	15.8	10.8

Table 7b. Experiment. A. Daphnia magna. Average egg-numbers
Analysis of Variance.

	N	Sum of Squares	Mean Square	VR.	Probability.
Rooms	2	430·8	215·4	9·463	$<\cdot001$
Crowding.	1	80·1	80·1	3·518	just $>\cdot05$
Interraction	2	50·9	25·5	1·119	$>\cdot2$
Error	42	956·0	22·8		
Total	47	1517·8			

Means:- 27°C = 9·07 ; 18°C = 15·83 ; 17°C = 14·34
Crowded = 11·57 ; Uncrowded = 14·15

Table 8. Experiment B. Experimental data.
(a) Daphnia magna.

	← 27°C →		← 16°C →	
Days	High Food	Low Food	High Food	Low Food
6	55/10	0/0	—	—
8	125/9	0/0	—	—
10	27/8	40/9	—	—
12	25/0	0/0	—	—
14	4/13	6/8	—	—
16	$144/10^{L}$	12/6	15/1	0/0
18	149/7	23/9	109/9	83/6
20	137/7	55/7	1/0	16/2
22	$159/8^{D}$	1/9	24/1	0/0
24	143/6	25/6	170/9	54/7
26	$87/5^{D}$	5/6	38/1	12/4
28	$115/5^{DD}$	$29/9^{DD}$	167/4	1/0
30	$48/2^{D}$	$11/5^{D}$	176/5	137/10
32	24/1	22/6	0/0	0/0
34	—	—	304/7	6/1

Table 8 b. *Ceriodaphnia dubia.*

	27°C				16°C			
Days	High Food		Low Food		High Food		Low Food	
6	90/7	79/3	78/10	59/6	—		—	
8	39/3	73/5	11/3	46/6	—		—	
10	22/4	35/3	32/6	6/1	—		—	
12	54/4	73/5	79/4	71/4	—		—	
14	64/4	110/8	78/7	64/8	2/1	4/1	2/1	7/1
16	83/8	41/3	54/10	64/9	7/2	7/1	3/1	2/0
18	55/7	26/5	33/10	36/8	11/2	2/1	12/2	10/3
20	59/8	81/9	47/9	54/9	8/1	16/2	0/0	7/1
22	85/10	40/8	46/11$^{\text{D}}$	26/8	26/4	0/0	16/4	25/5
24	36/10$^{\text{DD}}$	46/11$^{\text{DD}}$	31/8$^{\text{D}}$	31/9$^{\text{DD}}$	8/2	34/6	0/0	7/1
26	—		—		13/2	8/1	22/4	16/4
28	—		—		22/4	22/3	0/0	0/0
30	—		—		43/3	36/4	25/3	34/4
32	—		—		10/1	38/4	13/3	8/4
34	—		—		26/3	25/3	8/2	0/0
36	—		—		22/5$^{\text{DD♂}}$	16/4$^{\text{D♂DD}}$	21/4$^{\text{D♂}}$	27/3$^{\text{D♂DD}}$
38	—		—		2/1$^{\text{D♂D}}$	0/0$^{\text{D♂}}$	0/0	0/0
40	—		—		9/4	7/1	20/4	18/2
42	—		—		5/1	12/13	0/0	0/0
44	—		—		11/2$^{\text{D♂}}$	23/4$^{\text{D♂D}}$	33/3	19/3
46	—		—		12/2	19/2	0/0$^{\text{D♂D}}$	0/0$^{\text{DD♂}}$
48	—		—		13/3$^{\text{D}}$	23/2	35/3$^{\text{D♂}}$	14/2
50	—		—		7/1$^{\text{D♂}}$	16/1	0/0$^{\text{D♂}}$	0/0
52	—		—		20/3$^{\text{DD}}$	23/3$^{\text{D♂DD}}$	19/3$^{\text{DDD}}$	19/3
54	—		—		0/0	0/0	0/0$^{\text{D♂}}$	0/0
56	—		—		6/1	6/1	0/0	7/1

Table 8c. Daphnia pulex

	27°C				16°C			
Days	High Food		Low Food		High Food		Low Food	
9	$0/0^{DDDD}$	$5/1^{DD}$	$2/2^{DD}$	$7/3^{DD}$	—		—	
11	$0/5^{D}$	$3/3^{DD}$	$6/4^{D}$	$2/3^{DD}$	—		—	
13	$3/8^{DDD}$		$6/7^{DDDDD}$		5/1	44/5	26/4	22/3
15	$10/5^{DDD}$		$6/8^{DDD}$		35/3	14/2	10/2	9/3
17	$24/5^{DD}$		$0/5^{DD}$		33/6	34/5	12/4	37/7
19	—		—		3/1	19/2	13/4	7/1
21	—		—		59/6	0/0	27/2	32/5
23	—		—		0/0	17/3	33/3	23/3
25	—		—		19/3	28/4	1/1	5/1
27	—		—		27/4	6/2	20/5	0/1
29	—		—		$0/1^{DDD}$	$1/1^{DDD}$	$11/3^{DDD}$	$8/3^{DDD}$
31	—		—		2/2	6/6	$0/1^{DD}$	$10/5^{D}$
33	—		—		0/1	0/4	$13/3^{D}$	$6/4^{D}$
35	—		—		$0/2^{DDD}$	$8/3^{DD}$	0/0	$4/2^{D}$
37	—		—		11/2	$2/2^{D}$	$2/4^{DD}$	$0/0^{DD}$

Table 9. Experiment 8. Total young produced per 10 individuals.
(a) Daphnia magna

	27°C		16°C	
Days	High Food	Low Food	High Food	Low Food.
6	55	0	0	0
8	180	0	0	0
10	207	40	0	0
12	232	40	0	0
14	236	46	0	0
16	380	58	15	0
18	545·6	81	124	83
20	697·8	136	125	99
22	874·5	137	149	99
24	1053·3	162	319	153
26	1162·1	167	357	165
28	1326·4	196	524	166
30	1422·4	209·8	700	303
32	1482·4	241·2	700	303
34	—	—	1004	309

Table 9b. *Ceriodaphnia dubia*

	27°C		16°C	
Days	High Food	Low Food	High Food	Low Food.
6	79.5	68.5	0	0
8	135.5	97.0	0	0
10	164.0	116.0	0	0
12	227.5	191.0	0	0
14	314.5	262.0	5.4	9.5
16	376.5	321.0	18.2	15.3
18	417.0	355.5	30.8	40.3
20	487.0	406.0	52.2	47.3
22	549.5	442.0	78.2	92.3
24	590.5	478.6	110.6	99.3
26	—	—	130.2	142.8
28	—	—	170.6	142.8
30	—	—	243.6	208.0
32	—	—	285.2	232.3
34	—	—	332.0	242.3
36	—	—	367.4	295.5
38	—	—	368.4	295.5
40	—	—	388.4	350.5
42	—	—	409.6	350.5
44	—	—	452.2	423.4
46	—	—	498.8	423.4
48	—	—	553.4	505.1
50	—	—	591.8	505.1
52	—	—	623.4	568.5
54	—	—	623.4	—
56	—	—	723.4	—

Table 9c. Daphnia pulex

	27°C		16°C	
Days	High Food	Low Food	High Food	Low Food
9	2·5	4·5	0	0
11	4·4	9·5	0	0
13	7·1	14·1	24·5	24
15	19·6	21·6	49·0	33·5
17	67·6	21·6	82·5	58·0
19	—	—	93·5	68·0
21	—	—	123·0	97·5
23	—	—	131·5	125·5
25	—	—	155·0	128·5
27	—	—	171·5	138·0
29	—	—	172·0	148·0
31	—	—	177·7	155·2
33	—	—	177·7	173·2
35	—	—	183·4	177·6
37	—	—	198·8	178·8

Table 10 Experiment B. Total number of adult instars per 10 individuals.
(a) Daphnia magna.

	27°C		16°C	
Days	High Food	Low Food	High Food	Low Food
6	10	0	0	0
8	19	0	0	0
10	27	9	0	0
12	27	9	0	0
14	40	17	0	0
16	50	23	1	0
18	57·8	32	10	6
20	65·6	39	10	8
22	75·6	48	11	8
24	83·1	54	20	15
26	89·3	60	21	19
28	96·4	69	25	19
30	100·4	75·2	30	29
32	102·6	83·8	30	29
34		—	37	30

Table 10 b *Ceriodaphnia dubia*

Days	27°C		16°C	
	High Food	Low Food	High Food	Low Food.
6	5	8	—	—
8	9	12.5	0	0
10	12.5	16.0	0	0
12	17.0	20.0	0	0
14	23.0	27.5	1.8	2.2
16	28.5	37.0	4.7	3.5
18	34.5	46.0	7.6	9.0
20	43.0	55.0	10.2	10.0
22	52.0	64.5	14.2	20.0
24	31.2	36.8	21.2	21.0
26	—	—	24.0	30.0
28	—	—	30.6	30.0
30	—	—	36.9	37.8
32	—	—	41.3	455
34	—	—	46.8	48.0
36	—	—	55.1	56.0
38	—	—	56.4	56.0
40	—	—	62.4	64.4
42	—	—	66.6	64.4
44	—	—	73.1	73.1
46	—	—	78.1	73.1
48	—	—	84.4	83.1
50	—	—	87.2	83.1
52	—	—	97.2	95.6

Table 10c. *Daphnia pulex*

	27°C		16°C	
Days	High Food	Low Food	High Food	Low Food
9	·5	2·5	0	0
11	6·6	6·9	0	0
13	13·8	12·3	3·0	3·5
15	20·1	22·3	5·5	6·0
17	30·1	32·3	11·0	11·5
19	—	—	12·5	14·0
21	—	—	15·5	17·5
23	—	—	17·0	20·5
25	—	—	20·5	21·5
27	—	—	23·5	24·5
29	—	—	24·5	27·5
31	—	—	30·2	31·8
33	—	—	33·8	38·1
35	—	—	37·4	40·1
37	—	—	41·7	43·4

Table 11. Experiment B. Average Egg numbers.
(a) *Daphnia magna*.

	27°C		16°C	
Days	High Food	Low Food	High Food	Low Food.
6	5·5	—	—	—
8	13·9	—	—	—
10	3·4	4·4	—	—
12	—	—	—	—
14	2·2	·8	—	—
16	14·4	2·0	—	—
18	21·3	2·6	15·0	—
20	19·6	7·9	12·1	13·8
22	19·9	·1	12·5	8·0
24	23·8	4·2	18·9	—
26	17·4	·8	38·0	7·7
28	23·0	3·2	41·8	3·0
30	24·0	2·2	35·2	13·8
32	24·0	3·8	—	—
34	—	—	43·4	6·0
Means	16·3	2·9	27·1	8·7

Table II(b). *Ceriodaphnia dubia*

	27°C		16°C	
Days	High Food	Low Food	High Food	Low Food
6	16·9	8·6	—	—
8	14·0	6·3	—	—
10	8·1	5·4	—	—
12	14·1	18·8	—	—
14	14·5	9·5	3·0	4·5
16	11·3	6·2	4·7	3·0
18	6·8	3·8	4·3	4·8
20	8·2	5·6	8·0	7·0
22	6·9	4·0	6·5	4·6
24	3·9	3·6	5·2	7·0
26	—	—	7·0	4·8
28	—	—	6·3	—
30	—	—	11·3	8·4
32	—	—	9·6	3·0
34	—	—	8·5	4·0
36	—	—	4·2	6·9
38	—	—	2·0	—
40	—	—	3·0	6·7
42	—	—	4·2	—
44	—	—	5·7	8·7
46	—	—	7·8	—
48	—	—	6·0	9·8
50	—	—	10·2	—
52	—	—	7·2	6·3
Means	10·5	7·2	6·2	6·0

Table II(c). <u>Daphnia pulex</u>

	27°C		16°C	
Days	High Food	Low Food	High Food	Low Food
9	5·0	1·8	—	—
11	·4	1·1	—	—
13	·4	·9	8·2	6·9
15	2·0	·8	9·8	3·8
17	5·0	0·0	6·1	4·5
19	—	—	7·3	4·0
21	—	—	9·8	8·4
23	—	—	5·7	9·3
25	—	—	6·7	3·0
27	—	—	5·5	3·3
29	—	—	·5	3·2
31	—	—	1·0	1·7
33	—	—	0·0	2·7
35	—	—	1·6	2·0
37	—	—	3·3	·5
Means	2·6	·9	7·4+ 1·3*	5·7+ 2·2*

+Before infection with fungus *After infection with fungus.

Table II(d) Analysis of variance.

	N	Sum of Squares.	Mean Square	Vr.	Probability
Species	2	1482·6	741·3	27·771	<·001
Food	1	28·3	28·3	1·0609	>·2
Temperature	1	1069·7	1069·7	40·072	<·001
Spec. – Temp.	2	871·3	488·6	18·306	<·001
Spec. – Food.	2	1170·3	582·2	21·808	<·001
Food – Temp.	1	50·9	50·9	1·9079	>·2
Spec.-Food-Temp.	2	16·0	8·0		
Error	106	2829·6	26·7		
Total.	117	7524·6			

Table a Experiment B. Survival of *Ceriodaphnia dubia* and *Daphnia pulex* (in days)

Ceriodaphnia dubia				Daphnia pulex			
27°C		16°C		27°C		16°C	
High Food	Low Food	High Food	Low Food	High Food	Low Food	High Food	Low Food
24	22	36	36	9	9	29	29
24	24	36	36	9	9	29	29
24	24	36†	36†	9	9	29	29
24	24	36†	36†	9	9	29	29
26	26	36†	46	9	11	29	29
26	26	38	46†	9	11	29	29
26	26	38†	46†	11	11	35	31
26	26	38†	46†	11	13	35	31
26	28	44	48†	11	13	35	31
26	28	44†	50†	13	13	35	33
26	28	44†	52	13	13	35	33
26	28	48	52	13	13	37	35
28	28	50†	52	15	15	39	37
28	28	52	54†	15	15	39	37
28	28	52	60†	15	15	39	37
28	30	52	62†	17	17	41	37
28	30	52	64†	17	17	41	39
28	30	52†	64	19	19	41	39
28	30	62	64	25	25	41	39
30	32	70	68	25	25	41	39
Mean 26.5	27.3	45.8 49.3*	50.9 52.2*	13.7	14.1	35.4	32.6

*females only † males.

Analysis of variance

	N	Sum of Squares	Mean Square	VR	Probability
Species	1	7210	7210	196.4	<.001
Food	1	51	51	1.390	c.2
Temperature	1	17683	17683	481.2	<.001
Spec. – Temp.	1	6	6		
Spec. – Food.	1	132	132	3.597	>.05
Food – Temp.	1	11	11		
Spec.-Food-Temp.	1	106	106	2.916	<.1
Error	152	5576	36.7		
Total	159	30775			

Table 13. Experiment B. Frequency of moulting, and age of production of the first brood in three species of Daphniidae.

Species	Treatment	Frequency of moulting		Time of first brood
		Regression coefficient	* Increase per 10°C	Days
Daphnia magna	High Food 27°C	3·7485 ± ·0124	1·853	8·05
	16°C	1·8394 ± ·0144		14·40
	Low Food 27°C	3·5710 ± ·0074	1·901	8·89
	16°C	1·6316 ± ·0241		15·46
Ceriodaphnia dubia	High Food 27°C	4·6500 ± ·0250	1·664	c 4·0
	16°C	2·5410 ± ·0020		15·30
	Low Food 27°C	4·5089 ± ·0021	1·547	c 4·0
	16°C	2·6497 ± ·0707		15·91
Daphnia pulex	High Food 27°C	3·6375 ± ·0556	2·145	9·10
	16°C	1·5419 ± ·0030		11·19
	Low Food 27°C	3·7500 ± ·1575	2·089	8·87
	16°C	1·6315 ± ·0026		10·84

* Calculated for 10 individuals. Unit of time one day.

Table 14. Length of adult instars in various Cladocera.

Species	Treatment	Source	Instar Length Days
Daphnia magna	27°C. Crowded	Experiment A	3·31
" "	27°C. Uncrowded	" "	3·16
" "	17°C. Crowded	" "	4·23
" "	17°C. Uncrowded	" "	4·71
" "	27°C. High Food	Experiment B	2·67
" "	27°C. Low Food	" "	2·80
" "	16°C High Food	" "	5·44
" "	16°C Low Food	" "	5·85
" "	28°C.	McArthur & Baillie 1929	c 3·0
" "	25°C.	Anderson & Jenkins 1942	1·99 to 3·23
Daphnia pulex	27°C. High Food	Experiment B	2·75
" "	27°C. Low Food	" "	2·67
" "	16°C. High Food	" "	3·94
" "	16°C. Low Food	" "	3·77
Daphnia obtusa	25°C.	Fox, Hardcastle & Dresel 1948	2·17
Daphnia longispina	25°C.	Banta 1939	1·48 to 2·62.
Ceriodaphnia dubia	27°C High Food	Experiment B	2·15
" "	27°C. Low Food	" "	2·22
" "	16°C. High Food	" "	3·94
" "	16°C. Low Food.	" "	3·77

Table 15. Experiment C. Average egg-numbers of *Daphnia obtusa* with varying exposure to light.

Instar	8 hours light in 24						2 hours light in 24						0 hours light in 24						
	Beakers					Total	Beakers					Total	Beakers					Total	Total
	1	2	3	4	5		1	2	3	4	5		1	2	3	4	5		
1	9·67	9·67	10·67	8·00	10·33	48·33	8·67	10·33	9·67	8·00	8·00	44·67	8·00	6·67	8·00	10·67	9·50	42·83	135·83
2	10·67	9·67	7·33	12·00	7·67	47·33	6·00	7·00	7·33	8·00	10·33	38·67	6·00	6·67	11·00	5·33	5·50	34·50	120·50
3	7·67	9·67	8·00	8·67	9·00	43·00	7·33	4·67	5·67	7·00	7·33	32·00	5·67	6·33	10·00	6·33	5·00	33·33	108·33
4	10·00	11·33	9·33	9·00	8·00	47·67	9·67	6·67	7·67	9·33	7·33	40·67	7·00	7·33	6·00	8·00	11·00	39·33	127·67
Totals	38·00	40·33	35·33	37·67	35·00	186·33	31·67	28·67	30·33	32·67	33·00	156·00	26·67	27·00	35·00	30·33	31·00	150·00	492·33
Means	9·50	10·04	8·82	9·42	8·25	9·32	7·92	7·17	7·58	8·42	8·25	7·80	6·67	6·75	8·75	7·58	7·75	7·50	8·21

Means of instars:- 1st = 9·05 ; 2nd = 8·03 ; 3rd = 7·22 ; 4th = 8·51

Analysis of variance:

	N	Sum of squares	Mean Square	Vr	Probability
Light	2	37·94̇	18·97̇	7·7874	c. ·001
Instars	3	27·194̇	9·065	3·7207	·05 – ·01
Interaction	6	4·777̇	·7963		
Error	48	116·94̇	2·4363		
Total	59	186·861			

Table 16. Food and distribution of some Lake District Cladocera.

Species	Food-group	Abundance-fertility Coefficients *			
		Algae scarce Detritus ab.	Algae scarce Detritus scarce	Algae ab. Detritus scarce	Algae ab. Detritus ab.
Sida crystallina	a	3·1	4·3	15·6	15·0
Simocephalus exspinosus	a	0·8	0·0	4·2	3·4
Lathonura rectirostris	a	0·0	0·0	0·6	0·4
Peracantha truncata	a	1·5	0·3	4·7	5·1
Simocephalus vetulus	b	7·0	0·0	0·0	0·4
Eurycercus lamellatus	b	11·3	0·0	9·1	7·6
Alonopsis elongata	b	3·0	4·0	5·6	2·1
Alona affinis	b	1·9	0·0	0·6	0·0

ab. = abundant.

for Food-groups see text.

$$* \text{Coefficient} = \frac{\sum_0^n \text{egg-number value} \times \text{abundance}}{n}$$

n = Total number of habitats collected.

Other values awarded according to arbitrary scales, explained in text.

Table 17. % of algae and flagellates, normally less than 20 μ in longest diameter in various samples of total plankton in Regent's Park Lake, and some ponds.

Locality	Date	% Algae less than 20 μ
Regent's Park Lake	10. 11. 49	90·9
" " "	10. 12. 49	90·1
" " "	22. 12. 49	89·4
" " "	14. 1. 50	93·1
" " "	30. 1. 50	95·3
" " "	15. 2. 50	79·6
" " "	1. 3. 50	93·9
" " "	28. 3. 50	80·8
" " "	24. 4. 50	91·5
" " "	8. 5. 50	71·6
" " "	15. 6. 50	75·7
" " "	8. 8. 50	80·5
" " "	12. 10. 50	78·1
College Botany Garden, Pool 5	16. 1. 50	27·6
" " " " "	15. 2. 50	81·9
" " " " "	x. 3. 50	38·6
" " " " "	25. 4. 50	45·2
" " " " "	7. 6. 50	65·0
" " " " "	8. 8. 50	76·7
" " " " "	14. 10. 50	73·3
Waterlily Pond, Botany Garden	16. 1. 50	89·3
" " " "	15. 2. 50	0·0
" " " "	x. 3. 50	15·5
" " " "	25. 4. 50	5·0
" " " "	7. 6. 50	60·8
" " " "	8. 8. 50	87·5
Witt's Farm, God's Hill, Hants	8. 6. 50.	23·3

Table 18 Filtratory setae & setules in various species of *Daphnia*

Species	Animal	Distance between Setae (μ)	Setules (μ)
Daphnia magna	1	15·2	1·7
		14·7	1·7
		14·5	1·7
	2	15·0	·9
		12·3	·9
		11·7	·8
		11·4	·8
	3	10·9	·9
		10·0	—
		9·4	·7
	4 (young)	6·0	< ·5
		6·1	< ·5
		6·1	< ·5
		5·7	< ·5
	5 (neonatae)	c 3·0	< ·3
Daphnia atkinsoni	1	15·2	1·2
	2	16·7	—
	3	16·7	1·2
		12·3	1·4
Daphnia pulex	general observations	c.9 to 10 μ	—
Daphnia curvirostris	general observations	c 9 to 10μ	—
Daphnia obtusa	1	10·7	1·0
	2	10·4	·8
		9·6	—
	3	10·4	·8
		10·0	·9
		10·4	·8
		10·5	·8
Daphnia longispina	1	7·1	—
		7·6	·6
		7·4	—
Daphnia hyalina lacustris	1	6·3	—
		6·3	·6
	2	5·6	·6
		5·7	·6
		5·4	·6
		5·6	·6

The British Species of the Genus Daphnia

from D.S. Johnson

During research on the ecology of the Cladocera I have become convinced of the need of a comprehensive systematic account of the British species of the genus Daphnia O.F. Müller. The most recent British work which attempts a complete treatment is a paper by Brady (1898), which is neither reliable nor readily accessible. The key of Scourfield and Harding (1941) is good within its limits; but it is not possible to treat the genus adequately in a brief key. Moreover, our knowledge of British species has been increased considerably since 1941. The British student has thus to rely largely on foreign works, as those of Lilljeborg (1900), Keilhack (1909), Wagler (1936, 1937), and Rylov (1935), and the very comprehensive account of Richard (1896). Few of these are readily obtainable, and all are mor or less out of date. Recent work seems to have lessened considerably the chaos which characterises the systematics of the genus; but much of this work is not yet included in any general account.

A thorough review of the whole genus would involve years of special study, but it is possible for a field worker, with reasonable access to the literature, to provide a practical account of the species of a limited area, such as the British Isles. My aim in this paper is to provide such an account. Whilst I have drawn much on the work of previous authors, I have checked all characters as far as possible by careful examination of living or recently dead individuals. A very considerable number of preserved specimens has also been examined; but these are not usually so satisfactory for purposes of identification and study.

I cannot express too highly my indebtedness to the late D.J. Scourfield, whose recent publications have considerably lightened the task of arranging the British forms of the genus. I am especially indebted for the use of unpublished notes on *Daphnia curvirostris* Eylmann, which first directed my attention to this undoubtedly distinct species.

General consensus of opinion divides the genus *Daphnia* into two groups, which Wagler (1936) treats as two subgenera, *Ctenodaphnia* Dybowski and Grochowski 1895, and *Hyalodaphnia* Schödler 1866. Apart from the eclectic selection of names, this would appear to be a sound classification.

According to the international rules, the name of a sub-genus which includes the generic type must be the same as that of the genus. The second of Wagler's sub-genera thus becomes *Daphnia* O.F. Müller 1785, and its type *Monoculus pulex* (de Geer). Under no circumstances can *Hyalodaphnia* with type *Hyalodaphnia kahlbergensis* Schödler be available.

The distinctions between the two sub-genera are adequately summarized by Wagler. They are perhaps best shown in tabular form.

Ctenodaphnia	*Daphnia*
Fornices more or less strongly projecting and angular, or with a spine.	Fornices usually not strongly projecting, smoothly arched.
Secondary fornices usually present and sometimes very large.	Secondary fornices rarely present and if present, vestigial.
The dorsal portion of the head-carapace suture is directed	The dorsal portion of the head-carapace suture is directed posteriorly

anteriorly so that the carapace extends forwards into the head-shield, at least for a short distance.	so that the head-shield extends backwards, between the carapace valves.
The ephippium is sub-rectangular, and the egg-spaces are directed obliquely to longitudinally.	The ephippium is sub-triangular, the apex of the triangle being posterior; and the eggs are placed almost at right-angles to the dorsam.

Certain important characters have a distribution cutting across the boundaries of the sub-genera, and seem to be examples of parallel evolution.

Thus the claws lack combs in *Daphnia* (*Ctenodaphnia*) *lumholtzi*, and in the *longispina-cucullata* group of *Daphnia* s.s. Crests are found in some members of all sections of the genus, being absent in others. The inner ventral carapace margin bears oblique setae in at least the majority of species of the sub-genus *Ctenodaphnia* and in *Daphnia* (*Daphnia*) *obtusa* (see Scourfield 1943).

Sub-genus *Ctenodaphnia* Dybowski and Grochowski 1895.

Synonym:- *Dactylura* Brady 1898.

Three species of this sub-genus are recorded from the British **Isles:** *Daphnia magna* Strauss, *Daphnia atkinsoni* Baird, and *Daphnia psittacea* Baird. It is uncertain what species the last really is. It is possible that *Daphnia psittacea* Baird Auct. may occur here; but this is not certainly the same as Baird's species. It is best named *D. carinata v. similis* Claus,

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* Footnote

The aberrant Oriental and Ethiopian species *Daphnia lumholtzi* Sars approaches the sub-genus *Daphnia* in this feature, but in other respects it is a *Ctenodaphnia*.

and I have included it in the key, but not in the descriptions, under that name.

The species may be distinguished as follows:

1(2) ~~(a)~~ Dorsal edge of post-abdomen deeply emarginate, anal denticles in two groups — D. magna

~~(b)~~ Carapace only extending a short distance into the head-shield.

2(1) ~~(a)~~ Dorsal edge of post-abdomen not emarginate, anal denticles continuous. — 3

~~(b)~~ Carapace extending deeply into head.

3(4) ~~(a)~~ Carapace projection widening into a broad shield anteriorly (Fig. 3a) — D. atkinsoni

~~(b)~~ With characteristic supra-ocular depression or flattening (Figs. 2a, 3a)

~~(c)~~ Secondary fornix very well-developed, commonly exceeding half the carapace length (Fig. 2a)

4(3) ~~(a)~~ Carapace projection narrow throughout its length — D. carinata v. similis

~~(b)~~ No supra-ocular depression

~~(c)~~ Secondary fornix feeble, not nearly reaching half the carapace length.

Daphnia magna Strauss 1819-1820. Mem. mus. Hist. Nat. 6

Synonyms:- Daphnia schäfferi Baird 1850. Nat.Hist.Brit. Entomostraca, Ray Soc.

nec Daphnia pulex v. magna Strauss. Baird 1850. Nat.Hist.Brit.Entomostraca, Ray Soc.

Dactylura magna G.S.Brady 1898. Nat.Hist. Trans. Newcastle

B

Daphnia magna Strauss. Lilljeborg 1900. Cladocers Sueciae

Daphniamagna Strauss. Wagler 1936. Arch.Hydrobiol. Plankt. 30

Daphnia magna Strauss. Scourfield and Harding 1941. Sci. Publ. freshw. biol. Ass. 5.

This species is too well-known and well-characterized to need detailed description here. The characters given in the key distinguish it from all other species, except the aberrant D. lumholtzi Sars. This tropical species is never likely to be found in our area and could not be confused with D. magna.

The dorsal aspect of the head is very characteristic (Fig.1 b) and also the general form * (Fig. 1a.).

The antennule is of moderate size. The setules of the basal '~~Filtratory~~' endites of the thoracic limbs are stouter and less closely set than those of the 'pulex' group, being circa 12μ to 15μ apart.

The combs are long, with numerous teeth, and somewhat ill-defined.

This is the largest species of Daphnia in the British Isles. Exceptional individuals may reach 6 mm. in length, but the normal size range of old individuals is from 3 to 4 mms. Rarely old females are met with which are only 2.5 mm. long.

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* Footnote

Descriptions of species apply to parthenogenetic females except where otherwise stated.

The species is widely distributed in the S., E., and Midlands of England, though rarely common. In a few areas, as around London, it is not uncommon. It appears to be absent from the north and west of Great Britain and from Ireland.

Wagler (1936) gives its distribution abroad as all Eurasia from England to China and Japan, and south to N. Africa. He also records the species as occurring in Greenland (on the basis of Wesenberg-Lund's 1894 record); But Poulsen (1940) considers this doubtful. The species is not known from Iceland.

Wagler states that he knows of no records from N. America; but Birge (1916) ≠ gives several localities, and Brown (1929) speaks of it as occurring in the northern parts of the continent.

Portions of the carapace margin remain attached to the ephippium in this species, giving it a very characteristic appearance.

The male is much smaller than the female, being only 1 to 2 mms. long. The post-abdomen of the fully mature male has a characteristic and peculiar form, making it easily recognizable (Fig.1c). The anterior carapace bay is more pronounced than in most species of the genus. The peculiarities of the adult male develop gradually (Scourfield 1943), and male and female neonatae do not differ greatly.

Daphnia atkinsoni Baird 1859, Ann. Mag.Nat.Hist. (3) 4, 280-283.

Synonyms:- ? Daphnia psittacea Baird 1850. Nat.Hist.Brit.
Entomostraca, Ray Soc.
Daphnia bolivari Richard 1888. Bull.soc.Zool. fr.
B. 43

Daphnia crassispina Wesenberg-Lund 1894. Vidensk. Nedd.
naturl. Foren. **92**

Dactylura pubescens Brady 1898. Nat.Hist.Trans. Newcastle.
13.

Daphnia atkinsoni Baird. Lilljeborg 1900. Cladocera Sueciae

Daphnia triquestra G.O. Sars 1903. Ann. mus.Zool. Acad.Sc.
Russie 8.

? *Daphnia fusca* Gurney 1906. J. Asrav. Soc. Beng.

Daphnia atkinsoni v. nuda Keiser 1923. Bull. Univ. Asie
Central, 31-33.

Daphnia atkinsoni v. triquetiformis Keiser 1923. Bull. Univ.
Central, 2.

Daphnia atkinsoni v. turkomanica Keiser 1923. Bull. Univ.
Central, 2.

Daphnia atkinsoni Baird. Wagler 1936. Arch, Hydrobiol. Plankt.
30.

Daphnia atkinsoni Baird. Scourfield and Harding 1941. Sci.Publ
freshw. biol. Ass. **5.**

The species has usually a rather characteristic elongate oval form, and is not at all compressed. The head is small but considerably higher than in *D. magna*. The rostrum is somewhat blunt. The ventral margin of the head is almost straight. In the anterior margin there is a characteristic supra-ocular depression. Wagler describes this as more or less deep, but in my experience it may be very slight, particularly in well-fed individuals. The eye is large, with irregularly arranged lenses, and is placed near the anterior margin of the head. An ocellus is present. There is never any crest. The carapace is extended forwards dorsally, almost to the anterior margin of the head; and this projection broadens into a more or less extensive plate anteriorly (Fig. 3a). The fornices are very well-developed, and there are very large secondary fornices, normally attaining over half the carapace length. This feature alone is sufficient to distinguish D. atkinsoni from any other British species of the genus. At the junction of head and carapace, the dorsal margin shows a very distinct flattened saddle (Fig. 2a.).

The antennules are large and prominent, projecting postero-ventrally between the carapace valves (Figs. 2a, 3a.).

In mature parthenogenetic individuals the carapace is elongate-oval in shape. The spine is of moderate length to very short, or, rarely, absent. Wagler states that the dorsal carapace margin is only slightly arched. I find this to be an unreliable character. In all species of Daphnia the degree of arching of the dorsal margin is determined, to a great extent, by the number of eggs in the brood chamber. In my cultures of D. atkinsoni individuals with many eggs have the dorsal margin more or less strongly arched.

The dorsal and ventral margins of the carapace have numerous, long, closely set, overlapping spinules. In typical D. atkinsoni these extend forwards as far as the nuchal region; but in some forms (triquetra, bolivari, crassispina) they extend on to the 'head-shield.' I have not seen any such forms, and they appear to be unknown in the British Isles and western Europe, being characteristic of races living at the margin of the species' range.

The inner ventral carapace margin is emarginate and bears a row of oblique setae, which Wagler treats as a character of the species, but it occurs at least in most members of the sub-genus, including D. 'psittacea' (Wolski 1932).

The setation of the ~~filtratory~~ food collecting limbs is similar to that of D. magna, the setae being about 15μ to 18μ apart.

The post-abdomen (Fig. 2b) is well-developed, and almost uniformly tapering, but with a slight dorsal curve. The claws are comparatively short; the anal denticles small and weak. The combs are long, somewhat ill-defined, and with many fine teeth.

The species is smaller than D. magna. According to Wagler females may reach 4 mm. but a length of from 2 to 3 mm. is more usual, at least in W. Europe.

The ephippial female is very similar to the parthenogenetic, but the carapace is usually less elongated (Fig. 2a). Ephippial individuals are sometimes less than 2 mm. in length.

The male (Figs. 2c, 3c) is about 1 to 1.5 mm. long. The form of the post-abdomen, in which the papillae, on which the vasa deferentia open, are small and smooth, at once distinguishes it from the male of D. magna.

The species is rare in the British Isles and has so far been found only in the S. and E. of England and in Yorkshire. Abroad the main range of the species is the Mediterranean region, N. Africa and S.E. Asia. Less commonly it is found east to central Asia and Siberia, and north to Denmark and Sweden. If Gurney's D. fusca belongs to this species it reaches N. India. It is also known from Greenland (D. crassispina), and Iceland (Poulsen 1940). *

It has been suggested that this species is only accidental in northern countries, and unable to maintain itself in cool climates. My field and experimental observations show that this is not the case. In fact the species appears to be permanently established in such countries as England and Denmark, and certain races are definitely adapted to life at low temperatures, and are killed by temperatures far lower than those needed to kill most *Daphnia* species. Whatever factor restricts the spread of this species in the northern part of its range it is not temperature.

Daphnia psittacea Baird 1850. Nat. Hist. Brit. Entomostraca, Ray Soc.

In 1850 Baird described a *Daphnia* from Blackheath under the name of *D. psittacea.* The description and figures are not very complete, but the species intended is clearly either *D. atkinsoni* or a member of the *D. carinata* series. Its exact identity is not clear. Many authors, as Sars (1889) and Wagler (1936), think that it is a 'carinata' *Daphnia,* in which case it would be a synonym of *D. similis* Claus, as Wagler points out. This usage has been adopted by many European authors.

Others, as Scourfield (1903) and Scourfield and Harding (1941), are inclined to regard ~~as~~ *D. psittacea* as a synonym of *D. atkinsoni.*

Wagler states that there are three European species of the sub-

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* Footnote

It seems probable from Wagler's account that *D. dolichocephala* G.O. Sars is merely a geographic sub-species of *D. atkinsoni;* this species extends throughout Africa, S. of the Sahara.

genus: *D. magna*, *D. atkinsoni*, and *D. carinata.* Of these Baird's species is clearly not *D. magna.* Since Baird described both *D. atkinsoni* and *D. psittacea*, these are probably not identical. Thus *D. psittacea* Baird must be synonymous with *D. carinata* King. He claims that Baird's figures and descriptions agree with this conclusion.

Scourfield on the other hand believes that *D. psittacea* Baird is merely a badly described race of *D. atkinsoni.*

The question is important, since *D. psittacea* Baird 1850 has priority over both *D. atkinsoni* Baird 1853 and *D. carinata* King 1852.

I have examined Baird's figures and description, and conclude that his species is completely unidentifiable. The description, particularly as regards the form of the rostrum and the resemblance to *D. pulex*, strongly suggests *D. carinata*, but is not sufficient to be conclusive. The figure, though not accurate for either species, appears to me to be more like *D. atkinsoni.* There is a slight supra-ocular depression, and the antennules are large and projecting (in the text they are expressly stated to be larger than in *D. magna.*) On the other hand large secondary fornices are neither figured not described, and the specimen drawn is more like *D. carinata* in form than are most individuals of *D. atkinsoni.* *D.psittacea* as described is thus indeterminable; and the fact that Baird described both *D. psittacea* and *D. atkinsoni* is not relevant, since there is no evidence that he ever compared the two species.

In the circumstances *D. psittacea* Baird can only be treated as a *nomen vanum*, and the possible occurence of a 'carinata' *Daphnia* at Blackheath be left undecided.

Sub-genus Daphnia O.F. Müller 1785. Entomostraca sea Insecta

Synonyms:- Monoculus L (partim) 1758. Systema Naturae 10.
Hyalodaphnia Schödler 1866. Arch. Naturgesch. 32.
Cephaloxus G.O. Sars 1861. Forh. Vidensk Selsk. Krist.
s.g. Daphnia s.s. Lilljeborg 1900 (partim). Cladocera Sueciae
s.g. Hyalodaphnia Schödler. Lilljeborg 1900. Cladocera Sueciae
s.g. Cephaloxus Sars. Lilljeborg 1900. Cladocera Sueciae
s.g. Hyalodaphnia Lilljeborg. Wagler 1936. Arch. Hydrobiol Plankt. 30.

This sub-genus is much better represented in Europe than the preceding.

The following species occur in the British Isles: D. pulex (de Geer), D. obtusa Kurz, D. curvirostris Eylmann, D. ambigua Scourfield, D. longispina O.F. Müller, D. hyalina Leydig, and D. cucullata G.O. Sars.

It is usual to arrange the sub-genus in two groups; the 'pulex' group with combs on the claws, and the 'longispina-cucullata' group which lack combs. Even though the supposed intermediates between D. pulex and D. longispina advanced by Wesenberg-Lund (1926), Grese (1914), Alberici (1935) and others do not, in fact, exist, this grouping is still open to criticism. It is highly probable that the comb has been lost on several occasions. Such a species as D. ambigua for example may well be derived from a ctenate species rather than from D. longispina.

However, a regrouping of these species could only be successful after a thorough revision of the whole sub-genus. As I have neither time nor facilities for such a study, which would take a lifetime's work, I have adopted the old division for convenience. This does not imply that I accept it as natural.

The 'pulex' group.

As usually defined, this group includes all members of the sub-genus which possess true combs. On this definition no other characters can be advanced to distinguish the group as a whole. If the limnetic N. American forms are excluded (for an account of these see Wolterect 1933), a fuller diagnosis can be given, since the old-world species form a tolerably well-defined assemblage.

Races vary in form from those which are scarcely compressed, clumsily built, and opaque, to moderately compressed, slender, and semi-transparent forms. These features show little relation to specific limits. There is usually no crest of any kind, and if such a crest is present (as in D. pulex v. cristata) it is very low, and usually more or less dorsal in position. The rostrum is variable, but always reaches beyond the antennules. The antennules may be well-developed, small, or vestigial. They are always associated with a characteristic antennule mound. The carapace reticulations are always distinct. The carapace spine is rarely long and is often short or absent.

The combs show considerable variation. As Wesenberg-Lund has pointed out, they may be comparatively short and weak; but this is only so if comparison is restricted to members of the 'pulex' group. I know of no reliable descriptions of 'pulex' type Daphnia in which the comb could be described as rudimentary, even by the most imaginative systematist; and I have certainly never found such forms. Certain authors, as Wesenberg-Lund (1926), have indeed claimed to find combless individuals in populations of *D. pulex.* As Rammner (1933) points out, all these records are under suspicion, since mixed populations of *D. 'pulex'* and *D. longispina* in which the individuals are strikingly similar are by no means uncommon, and all records can be explained on this basis. Grese (1914) claims to have found populations showing all variation from a well-developed comb, to its complete absence. For the most part his paper is not very convincing, and no other author seems to have seen such a population. Unfortunately he only describes the variation in the combs and does not attempt to correlate it with other features of the animals. Thus it is impossible to tell with how many species he was concerned, or what these species were. Unless this work be confirmed, it must be ignored. His claim to have found an individual with a comb on one claw and none on the other, would be an interesting example of a mutation, if not an error.

I recognize three species of the group in this country. They can be distinguished as follows:

1 (2) (a) Antennule mound short and high (Figs. 7a, 7b) *D. obtusa*
(b) Inner ventral margin of carapace with a shallow median emargination, bearing a short row of long setae directed obliquely inwards and posteriorly (Fig. 7c).

2 (1) (a) Antennule mound long and low (Figs. 4a, 4c) 3
(b) Inner ventral margin of carapace not emarginate; these setae lacking.

3 (4) (a) Antennule large and projecting (Fig. 4a) *D. pulex*

(b) Combs on claws with comparatively few coarse teeth (Usually 4 to 6 indistal; 4 to 8 improximal: Fig. 5a)

(c) Abdominal processes setose

4 (3) (a) Antennule vestigial (Fig. 4c) *D. curvirostris*

(b) Combs on claws with more numerous, fine teeth (distal 8 to 13; proximal 10 to 16: Fig. 5b)

(c) Abdominal processes without setae or with very few setae.

Some of these characters are slightly variable, but there is not sufficient variation to make specific determinations impossible.

Daphnia pulex (de Geer), emend. Scourfield 1942. Ann.Mag.Nat.Hist.(11) 9.

Synonyms:-[*]*Monoculus pulex* L (*Partim*)1758.Systema Naturae 10th Edit

Monoculus pulex de Geer 1778. Mem. pour servir à l'histoire naturelle des insectes. 7, 442.

Daphnia pulex (de Geer). Baird 1850 (*partim*). Nat. Hist.Brit. Entomostraca, Ray Soc.

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[*] Footnote

A complete synonymy of this species cannot be given since many descriptions are quite inadequate. *D. pulex* (de Geer), auct., may stand for any or all of the three forms considered here. In the absence of good figures or other indications, forms so named are indeterminable. Since it is possible that still other species have been confused with these, authors would do well to provide such indications for races with which they deal.

Daphnia pulex v. magna Strauss. Baird 1850. Nat. Hist. Brit. Entomostraca,
Ray Soc.

Daphnia middendorfiana Fischer 1851. Zoologie Wirbellose Tiere **2.**

Daphnia schoedleri G.O. Sars 1861. Forh. Vidersk Selsk. Kr. st.

Daphnia pennata G.O. Sars 1861. Forh. Vidensk Selsk. Kr. st.

Daphnia minnehaha Herrick 1884. Final Report Crustacea of Minnesota.

Daphnia greenlandica Wesenberg-Lund 1895, Vidensk. Medd. natur.

Daphnia pulex (de Geer). Brady 1898 (*partim*). Nat. Hist. Trans.
Newcastle. **13.**

Daphnia schoedleri Sars. Brady 1898. Nat.Hist. Trans. Newcastle. **13.**

Daphnia hamata Brady 1898. Nat. Hist. Trans. Newcastle. **13.**

Daphnia wierzejskii Litynski 1913. Bull. Acad. Sc. Graco.

Daphnia pulex (de Geer). Birge 1918 (principally). Ward & Whipple,
Freshwater Biology.

Daphnia pulex (de Geer). Berg 1931 (*partim*). Vidensk. Medd. natur.
Forenh. Kbh. **92.**

Daphnia pulex (de Geer) Rammner 1933 (*partim.*) Zool.

Daphnia pulex v. cristata Rammner 1933. Int. Rev. Hydrobiol. **29.**

Daphnia pulex pulex (de Geer). Wagler 1937 (principally). Die Tierwelt
Mitteleuropas **2.**

Daphnia pulex (de Geer). Rylov 1935 (*partim*). Die Binnengewasser **15.**

Daphnia pulex (de Geer). Poulsen 1939, 1940. Zool. Iceland **35,** Medd.
Grönland **121.**

Daphnia pulex (de Geer). Scourfield and Harding 1941 (*partim*). Sci. pub.
freshw. biol. Ass. **5.**

As originally understood this species included all the non-cristate members of the sub-genus which possessed combs. Indeed some early authors, as Baird (1850), included *D. longispina* O.F. Müller in the species. Later a very considerable number of species and varieties was separated out. Most were insufficiently described and the characters relied on (small differences in length of shell spine, head-form, dorsal outline, colouration etc.) were for themost part unreliable. There has thus been a tendency to fuse these species, as tendency which has now gone too far. Most modern authors , as Birge (1918), include here all heavily built members of the sub-genus, in which a comb is present, and the crest absent or very slight. Other authors, as Woltereck (1933), have gone further and included the peculiar American limnetic forms of the '*retrocurva*' type. Some authors have even merged *D. pulex* and *D. longispina*, certainly an incorrect proceeding.

Whatever may be the status of the peculiar American plankton forms, it is extremely unlikely that any of them are conspecific with *D. pulex* s.s., and there is certainly no justification for including them here without further study.

The status of less aberrant members of the '*pulex*' complex is more obsuure. Some of these, such as *D. schoedleri* and D. *middendorffiana*, are form variations, rightly disregarded by most authors, and not meriting even varietal status. Others however are more distinct, and a few, such as *D. obtusa*, have been recognized, at least as varieties, by most authors, though sometimes on inadequate grounds.

Scourfield (1943) redescribed *D. pulex* and *D. obtusa*, and showed that they were very distinct species. In this paper he indicated that there were other species which had been confused with D. pulex and which he intended to describe later. He was prevented by his death from doing so, but I possess manuscript notes made by him on D. curvirostirs Eylmann which show that this is also a distinct species. I have been able to confirm that there are three distinct species in the British Isles. All forms that I have collected or seen can be ascribed to some one of these without any doubts. Unfortunately the only forms of the group which I have seen from abroad correspond with D. pulex s.s. so that I am not able to comment on the constancy of the other species outside Great Britain.

D. pulex as thus restricted contains comparatively large forms (1.5 to 4.0 mms.). They are slightly to moderately compressed. The head is moderately large. The rostrum is variable but never very long, and never short or upturned. The antennules are well-developed and projecting. They are inserted on along low mound, which may or may not reticulate (Fig. 4a.). The angle of insertion appears to differ slightly from that in D. obtusa. The ventral head margin is always somewhat concave, but the exact shape is variable, depending partly on the state of nutrition.

The carapace is sub-rectangular to oval. The reticulations are always distinct. The inner ventral margin runs parallel to the outer, is without emargination and is non-setate. The spinnules on the dorsal and ventral margins are numerous; usually more than 25, often 50 or more, in a row. They are comparatively long and slender; always exceeding half the interspace, and usually overlapping. The carapce spine is very variable. It usually exceeds 1/5 of the carapace length, but may be absent.

The '~~filtratory~~ collecting' setae are moderately fine and closely set (circa 9 - 10 μ apart).

The abdominal processes are more or less markedly setose. The post-abdomen is large, and shows a more or less distinct bay in the dorsal margin, proximal to the anal denticles. The anal regions is very slightly convex, sometimes showing a slight emargination. The anal denticles are 12 to 20 in number, but usually more than 15. They increase very gradually in size from proximal to distal, and the most distal is not longer than those preceding it (Fig. 5a.).

The combs are strong and conspicuous, the teeth stout. The distal comb has 3 to 6, more rarely 8, teeth. The proximal usually has 6 to 8 teeth, but may have as few as 4 (Fig. 5a).

The ephippium is typical of the sub-genus. Its dorsal ridge bears numerous, scattered, very fine, small, spinules.

The male is easily recognizable by the very well developed second abdominal process, which protrudes from the carapace. The post-abdomen usually shows a distinct bay as in the female. The short flagellum of the antennule (Fig. 10c) (2 to 3 times the olfactory setae) is also distinctive.

There would appear to be no valid varieties that certainly belong to this species unless D. groenlandica be so considered. The somewhat heavy form and deep brown pigment of this variety are characteristic of arctic races. These features are shown by other arctic Daphnia, but the name might perhaps be retained to draw attention to the problem.

D. minnehaha Herrick represents a curious mutation, which usually affects whole populations. In the young of these there is a long low crest on the dorsal margin of the head, which bears 1 to 5 small 'hooklets' (Fig. 4b). The adults have 'normal' pulex contours, though sometimes a slight angle remains in the nuchal region. Such forms are rarely recorded in the literature, but are probably not very rare. Unless young individuals are carefully examined they are likely to be overlooked. I have found a strain, probably of this species, with these features at Thetford, Norfolk, but know of no previous records for this country. Though the form is well-marked it is probably not worthy of a name, since parallel mutations occur in other species of *Daphnia*.

The length of the spine which has in the past been used to distinguish varieties, is influenced by many factors such as nourishment, age, and size of habitat. The same is true of head form. This is largely dependent on nutrition as Berg (1931) has shown. The form *D. middendorffiana* appears to be merely an extreme hunger form of *D. pulex*.

In the British Isles the species appears to be generally distributed, though absent from several northern and western districts, as for instance the English Lake District.

The species appears to be generally distributed over all temperate parts of the world. It is however not possible to give an exact picture of its distribution. I, myself, have seen specimens from Denmark and from Bear Island, but judging from published figures, it is widely distributed in Europe and the only form which occurs in the arctic.

Daphnia obtusa Kurz, emend. Scourfield 1942. Ann. Mag. nat. Hist. (11) **9.**

Synonyms:- * *Daphnia obtusa* Kurz 1874. Arch. naturw. Landesforsch. Böhm **3.**
Daphnia brevispina Daday 1888. Crustacea Cladocera Faunae Hungaricae.
Daphnia ornata Daday 1888. Crustacea Cladocera Faunae Hungaricae.
Daphnia alpina Daday 1888. Crustacea Cladocera Faunae Hungaricae.

Daphnia jurinei Stingelin 1895. Rev. suisse Zool. 3.

Daphnia propinqua G.O. Sars 1895. V. d. Selsk.

Daphnia pulex v. obtusa v. brevispina Daday. Brady 1898. Nat. Hist. Trans. Newcastle 13.

Daphnia pulex v. obtusa v. propinqua G.O. Sars. Brady 1898. Nat. Hist. Trans. Newcastle 13.

Daphnia pulex v. obtusa-obtusa Litynski 1913. Bull. Acad. Sc. Craco.

Daphnia tenuispina G.O. Sars. 1916. Ann. S. Afr. Mus. 15.

Daphnia pulex (de Geer). Berg.1931 (partim) Vidensk. Medd. naturh. Ferh. Kbh. 92.

Daphnia pulex v. obtusa Kurz. Wagler 1936. Arch. Hydrobiol. Plankt. 30.

Daphnia pulex v. obtusa Kurz. Wagler 1937 (partim) Die Tierwelt Mitteleuropas 2.

Daphnia pulex v. obtusa Kurz. Rylov 1935 (partim) Die Binnen gewasser 15.

Daphnia obtusa Kurz. Scourfield and Harding 1941. Sci. Publ. freshw. biol. Ass. 5.

Daphnia obtusa Kurz. Scourfield 1942. Ann. Mag. nav. Hist. (11), 9.

nec. Daphnia pulex v. obtusa Kurz. Stephanides, 1948. Survey freshwater biology of Corfu.

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* Footnote

As with D. pulex it is impossible to give a full synonymy of this species. As used at the present day the name may cover variants of all non-lacustrine species in the group.

Daphnia obtusa Kurz as redefined by Scourfield (1943) is a very distinct species, possibly not even closely related to D. pulex. On the whole it is a smaller species. Adult females range in size from 1.5 to 3.5. mms., but individuals more than 2.5 mms. long are rare. It is rarely much compressed. The head is comparatively small. The ventral margin is variable but more or less concave. The rostrum is commonly short, and typically has a characteristic upturned appearance (Fig. 7a). More rarely it approaches the typical form of D. pulex. The antennules are of moderate length, but shorter than in D. pulex. They arise from the ventral end of the antennule mound, and tend to be directed parallel to the rostrum. The antennule mound is short and high. It may or may not be reticulate (Figs. 7a, 7b).

The carapace is usually more slender than in D. pulex and more or less oval in shape. The inner ventral carapce margin has a shallow emargination, in the middle of its course, which bears a short row of setae, directed obliquely inwards and posteriorly (Fig. 7c). In this feature D. obtusa agrees with most members of the sub-genus Ctenodaphnia, but appears to be exceptional in the sub-genus Daphnia. Scourfield suggested that this character might be an adaptation to the more turbid environment in which the species lives. It seems to me to be more likely that it is a primitive character in the genus since it also occurs in species of the allied genus Cerrodaphnia which are not found in particularly turbid habitats. The spinules on the dorsal and ventral margins are few in number, normally much fewer than 25, and sometimes, though rarely, absent altogether. The shell spine is extremely variable. It is usually short, but may reach half the carapace length. Comparatively rarely it is completely absent. The commoner races of D. obtusa and D. pulex in this country are indistinguishabl on the basis of spine length.

The setae of the ~~filtratory~~ collecting limbs are circa 9.5 to 11.2 apart.

The abdominal processes are setose, usually exceedingly so. The post-abdomen (Fig. 5c) is smaller than in *D. pulex*; its dorsal margin forms a characteristic smooth convex curve. The anal denticles, usually 10 to 15 in number, are comparatively uniform in size, and their tips also lie on a marked curve. The combs of the claws are finer and their teeth more numerous than in *D. pulex*. The distal has normally 6 to 10, rarely more, teeth; the proximal usually about 10 to 12.

The male (Figs. 6c, 10a) is distinguished from that of *D. pulex* by the much shorter 2nd. abdominal process, which only projects slightly if at all from the carapace. The dorsal margin of the post-abdomen has no bay. The flagellum of the antennule is 3 to 4 times as long as the longest olfactory seta (Fig. 10a).

The species appears to be rather constant in its characters, the only striking variations that I have noticed being in the length of the spine, and in the shape of the rostrum.

In the British Isles it is widely distributed, but it is absent from many areas in the north and west. In my experience it is very much commoner than *D. pulex* and appears to be the commonest of the 'pond' *Daphnia* species. On the whole it inhabits smaller and shallower habitats than *D. pulex*. It is often associated with *D. curvirostris*. Despite their occurrence together, hybridization between these species is either very rare or absent. This is particularly clear in the case of *D. obtusa* and *D. curvirostris*. I have on several occasions carefully observed mixed sexual populations of these two species, over considerable periods; but I have not seen a single individual which could honestly be described as a hybrid or as an intermediate.

It is not possible to ascertain the full distribution abroad. It appears to be absent in the arctic, but common in temperate regions both of the northern and southern hemispheres.

Daphnia curvirostris Eylmann emend.

Synonyms[*]:- *Daphnia curvirostris* Eylmann 1886. Ber. naturf. Ges. Freiburg i (1) **2**.

Daphnia pulex v. curivirostris Eylmann, Birge 1916. Ward & Whipple, Freshwater, Biology.

Daphnia pulex (de Geer) Scourfield and Harding 1941 (partim) Sci. Publ. freshw. biol. Ass. **5**.

Daphnia pulex (de Geer) Scourfield 1942 (partim). Ann. Mag. Nat. Hist. (11), **9**.

Daphnia pulex v. obtusa Kurz. Stephanides 1948. Survey freshwater biology of Corfu.

Ekman's description, though accurate, is incomplete, and does not allow for variation.

In the manuscript note referred to above D.J. Scourfield gives the following characters as being distinctive of *D. curvirostris*:

The head is much as in *D. pulex* but the rostrum, when typically developed, is very long and recurved. The antennules are reduced to the olfactory setae and a small lateral seta, arising directly from the rostrum

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[*] Footnote

This species has been ignored by most authors, and no full synonymy can be attempted.

base, just anterior (ventral) to a long, usually low, reticulate mound (Fig. 4c).

The inner ventral margin of the carapace is as in *D. pulex.* The dorsal and ventral margins of the carapace have comparatively few spinules, usually less than 25. These spinules are usually short and only rarely as long as the inter-spaces.

The abdominal processes are devoid of setae. The combs (Fig. 5b) are somewhat longer than in *D. pulex* and consist of numerous fine teeth.

The dorsal ridge of the ephippium is quite smooth and devoid of spinules. During my research I have collected and observed several strains of this species, the identification of some of which was confirmed by Scourfield himself. I have thus been able to confirm and amplify Scourfield's characters and have found them to be constant.

The rostrum is somewhat variable. At its shortest it is like that of *D. pulex,* but when typically developed it is quite distinct. In shape it is somewhat reminiscent of that of *D. longispina.* The antennules are virtually non-existent apart from their setae, but there is a small oblique elevation, precisely comparable to that in *D. longispina* from which the setae spring. The antennule mound may be very low indeed or fairly high, but it is always distinguishable. It is almost invariably reticulate.

The carapace is usually oval. The carapace spinules are often very short and almost always very stout. The carapace spine is variable but is usually short and often absent, especially in old individuals.

The abdominal processes are often completely devoid of setae, but commonly there are a few extremely fine scattered setae, never sufficient to justify the term setose. The post-abdomen (Fig. 5b) is of moderate size; the distal portion is uniformly tapering, the dorsal margin almost straight.

The anal denticles increase rather rapidly in size distally. The most distal is the largest and the tips lie more or less on a straight line. The combs are finer than those of D. pulex, and also than those of D. obtusa. The proximal combhas about 10 to 16 teeth and the distal about 8 to 13.

The ~~filtratory~~ collecting setae are circa 9 - 10 μ apart.

The male, in the races I have seen (Figs. 6a, 6b, 10b) has a quite distinctive structure. The extreme reduction of the abdominal processes is very noteworthy. The flagellum of the antennule is very long, reaching more than 5 times the length of the longest olfactory setae. (Its termination is somewhat dilated, to a certain extent recalling D. ambigua.) The peculiar conformation of the anterior portion of the ventral carapace margin also appears to be characteristic. It would seem to be an exageration of the usual structure in the genus but strongly recalls this region in both female and male Scapholeberis. The combs are finer than thoseof D. pulex, and also than those of D. obtusa. The proximal comb has about 10 to 16 teeth and the distal about 8 to 13.

The peculiar hooked rostrum figured has been present in allmales that I have examined carefully. Judging from his figures it is also present in some at least of Stephanides' Corfu form (1948) which is certainly this species, and it was probably also present in Eylmann's form.

The setae on the ventral margin are not very conspicuous. They are all directed posteriorly, save for the few most anterior ones. The carapace spinules are more numerous than is usual in D. obtusa, but less so than in D. pulex. Those on the ventral margin are 20 to 30 in number. The most anterior ventral spinules are strikingly stout.

The exact relationships of this species are not clear. As indicated in the description it combines in an eclectic fashion features of D. obtusa and D. longispina along with peculiar characters of its own.

In the shape and structure of the rostral region, the non-setose abdominal processes, the form of the post-abdomen, and the nature of the anal denticles, it approaches very closely to D. longispina. In these features it shows much less resemblance to D. pulex, though in some of them it is intermediate between this species and D. longispina. The inner ventral carapace margin is as in D. pulex and D. longispina. In none of these features does it show any resemblance to D. obtusa. On the other hand, the combs, the spinulation of the carapace margins and the form of the male antennule are approached most nearly by D. obtusa. It also resembles this latter species more closely in size and general build, and in habitat.

The special features of the male seem to be quite unique.

The possibility that it might be a hybrid must be rejected. That it may be a true species of hybrid origin, comparable to those known in angiosperms, is possible, though unlikely. The characters remain constant, and there is no segregation of characters in the post-ephippial generation. The species does not appear to interbreed with D. pulex and D. obtusa.

That D. curvirostris comes near to the 'pulex' stock from which D. longispina originated seems not at all unlikely. Such features as the character of the rostrum and the nature of the post-abdomen and anal denticles, seem to me to be significant resemblances. However, the characters of the male show a marked divergence.

Its relationship to D. pulex and D. obtusa can perhaps best be represented by regarding these three species as three distinct lines of descent from a common ancestral stock. Each species shows a different combination of advanced and primitive characters, and no one can be considered as more primitive than the others.

It is virtually impossible to ascertain the distribution of this species. Scourfield thought that it was predominantly coastal; but I have found it in abundance at Aldwarke, Yorks, which is more than 40 miles, from the nearest sea coast. In my experience it is very common in certain areas, such as around London and in S. Yorks, and it is probably generally distributed in S. & E. England. It appears to be confined to very shallow waters. Abroad it is known from N. America and Europe but has been much confused with *D. pulex* and *D. obtusa*. A recent record of *D. pulex v. obtusa* in Corfu (Stephanides 1948), certainly refers to this species.

The '*longispina-cuculata*' group

This group as here defined includes all members of the sub-genus in which the claws lack true combs. With the exception of such forms as *D. ambigua* it forms a fairly homgeneous and possible natural group.

The forms included here are all somewhat compressed, often highly compressed. They are usually slenderly built. The carapace is normally very transparent; the reticulations often indistinct. The carapace spine is long in most races (not in *D. ambigua.*) The inner ventral carapace margin is never emarginate and never bears setae.

The ocellus is always very small. The antennules are small of vestigial. The post-abdomen is almost always small and comparatively feebly armed. The abdominal processes have few or no setae.

Forms with conspicuous crests and helmets are very common, and have given rise to great systematic difficulties.

Races of *Daphnia longispina* have been described which are said to approach *D. pulex* in possessing a rudimentary comb (see Wesenberg-Lund 1926; Baldi 1932). Such apparent intermediates have led some authors (as Keilhack 1909) not merely to abandon the division of the sub-genus into groups, but to suggest that *D. pulex* and *D. longispina* are not separable. Rammner (1933) examined the evidence and concluded that the so-called intermediate forms did not exist, being mostly based on misinterpretations. An apparent comb may be found in races of *D. longispina* formed by the coarsening and setting off of some of the most proximal danticles of the claws; but this is very different from the true comb of *D. pulex*. Most of the presumed intermediates are of this character. Rammner notes the occurence of mixed populations as a possible source of confusion. He considers the results of Grese (1914; see above) to be inadmissible. Rammner gives supplementary characters to distinguish the two species, including, the setation of the abdominal processes, the convex (*D. pulex*) or the conave (*D. longispina*) dorsal margin of the post-abdomen, and the nature of the 4th spine of the endopodite of the 2nd thoracic limb. However, Alberici (1935) does not accept Rammner's conclusions. She claims that his distinguishing features do not hold for a race of *Daphnia* from Monte Rosa which she persists is truly intermediate.

My own observations confirm those of Rammner, in so far as they show that the supposed intermediates do not really approach *D. pulex*. In mixed populations of *D. pulex* and *D. longispina* the two races may be remarkably similar; but wherever such populations have been accurately described there is always a clear distinction with no intermediates. Races of *D. longispina* and occasional individuals often show an incipient comb of the type described by Rammner, but in my opinion this bears no resemblance to the structure in D. pulex. I have examined carefully specimens of a supposed intermediate race from the Lago di Monscero, Domodossola, Italy, kindly sent to me by Dr. Vittorio Tonolli, and of a more extreme race from Loch on Moor in S. Uist. The former are almost typical D. longispina and show no approach whatsoever to any of the 'pulex' species. The latter are peculiar in some features, but again show no resemblance to a 'pulex' type Daphnia. Berg's race from Denmark is another form of this type. A further source of confusion, unknown to Rammner, is the occurence of several species which have in the past been called D. pulex. I have already pointed out the strong resemblance between D. curvirostris and D. longispina. Unless attention were paid to all characters it would be just possible for a worker to identify specimens of D. curvirostris as comb-bearing D. longispina.

Unfortunately the characters that Rammner uses to distinguish the two species are quite unreliable, and seem to have misled Alberici. In the setation of the abdominal processes and the form of the post-abdomen, D. curvirostris and D. longispina are prdably indistinguishable. Considerable further investigation seems to be indicated before the character of the 4th spine of the endopodite of the 2nd thoracic limb can be accepted as of systematic value. Nevertheless D. longispina is separable from D. curvirostris as comparison of my descriptions will show. It bears no resemblance to any other 'pulex' Daphnia. Suggestions that D. longispina can be united with D. pulex thus seem to lack any real foundation.

The close similarity between D. longispina and D. curvirostris does however cast doubt on the validity of dividing the sub-genus into two groups; and as explained above these are retained here merely for convenience in discussion.

Four species of the '<u>longispina-cucullata</u>' group are recorded from the British Isles. They may be distinguished as follows:-

1 (2) (a) Dorsal and ventral carapace margins normally without spinules in the adult. Spine very short or absent. — <u>D. ambigua</u>

(b) Head form characteristic (Figs. 8a, 8b.)

2 (1) (a) Carapace margins with spinules in the adult. Spine long, never, normally, absent. — 3

(b) Head not of this form.

3 (6) (a) With pigmented ocellus — 4

(b) Rostrum long.

4 (5) (a) Adults with no crest, or at most a rudimentary crest, at all seasons. — <u>D. longispina</u>

(b) Rostrum of characteristic form (Fig. 9a).

(c) Shell reticulations more or less well-marked.

5 (4) (a) Adults with a definite crest, at least in summer — <u>D. hyalina</u>

(b) Rostrum not of this form

(c) Normally very hyaline and highly compressed, Carapace reticulations feebly marked.

6 (3) (a) Ocellus invisible, without pigment, save in rare instances. — <u>D. cucullata</u>

(b) Rostrum short, effactory setae inserted at its apex.

Daphnia cristata (G.O. Sars), distinguished from *D. cucullata* by its long rostrum is not likely to occur in the British Isles.

Daphnia ambigua Scourfield 1946. J. Queckett micr. Club (4), **1**.

Synonyms: ? *Daphnia friedeli* Harturg W. 1896 Brandenbargia p.370.

As it is impossible owing to the inadequacy of the description, to say whether or no Harturg had this species, I prefer to use Scourfield's name.

The species was described from specimens collected in Kew Gardens. It was subsequently re-discovered, in the summer of 1947 in Regent's Park Lake by Professor H. Munro Fox (Fox 1948). It has not been found there since, despite a continuous search. However, in the summer and autumn 1950 it has appeared in numbers in the large pool in Queen Mary's Garden, Regent's Park (this is the site of the old Botany Garden.) I have examined numerous individuals from this habitat, both collected directly and taken from cultures; I have thus been able to confirm Scourfield's description and am convinced that this is a distinct species.

The small head has a very characteristic shape, somewhat resembling that of *D. obtusa* which the species also resembles in general form (Fig. 8a). The rostrum is short and blunt and somewhat upturned in the adult (Fig. 8b). The antennule is small but larger than in the other mebers of the group, and is noticeably projecting (Fig. 8c). There is no antennule mound. The basal plate of the head is exceptionally short and broad.

The eye is exceptionally large, almost filling the anterior portion of the head. The lenses are numerous and very regularly arranged.

Scourfield does not mention the ocellus but does show a minute ocellus in his figures. In my specimens the ocellus is not visible in most, but a very few individuals have a very minute pigmented ocellus. This is comparable to the situation in some races of D. cucullata.

Old individuals completely lack the carapace spine, but a very short spine may be present in young adults.

The inner ventral margin of the carapace is as in other members of the group. The dorsal and ventral margins of the carapace are completely devoid of spinules in most adults and all old adults.

The post-abdomen is somewhat more rounded distally than in D. longispina, approaching D. obtusa in this respect. The abdominal processes are almost, in my specimens quite devoid of setae. Processes 1 and 2 are fused for about one-third to half their length (Fig. 8d), this fusion being much more extensive than is normal in D. longispina. Scourfield's figures show a distinct process 4, but in my specimens this is either vestigial or absent. The anal denticles are 8 to 12 in number and very slender. They show a marked increase in size distally, though less so than in D. longispina and D. curvirostris. The claws are as in D.longispina.

The primiparae are from .8 to 1.0 mm. long and old individuals may reach to 2.2 mm.

The ephippial females are as in other species of the genus, smaller, not greatly exceeding 1.0 mm. The ephippium differs slightly in its detailed conformation from that of D. longispina. Its dorsal surface has minute scattered prickles, recalling those of D. pulex.

The neonatae are less aberrant. The characteristic head form is lacking. There is a rather long spine. The dorsal and ventral carapace margins have a considerable number of very slender spinules. The number of spinules and the length of the carapace spine decrease with each moult. In my experience these two processes are not perfectly synchronized and either spine or spinules may disappear first.

The male differs considerably from that of D. longispina. It is about 0.8 mm long. Carapace spine and spinules are retained throughout life. The antennules are well-developed. The flagellum is very long for this group, being comparable to that of D. pulex, (Fig. 10d). The structure of the flagellum (Figs. 10d, 10e) is very distinctive, especially the median widening and the 'spoon' tip.

The abdominal processes are much as in the female, though the first is somewhat reduced.

The known localities are large pools and lakelets. The species has only been found in summer and autumn. The distribution strongly suggests that this is an introduced species, as Fox (1948) concluded. However, its origin must remain obscure, until more is known of tropical species.

The relationships of the species are obscure. Scourfield considered that it came nearest to D. longispina, but the possibility that it has originated independently from D. obtusa or some similar species cannot be overlooked. There are also striking and perhaps significant resemblances to D. cucullata.

Daphnia longispina O.F. Müller. 1785 Entomostraca sea Insecta Festaecea.

Synonyms:* Daphnia pulex var. Baird 1850 Nat.hist.Brit.Entomostraca.
Ray Soc.

Daphnia paludicola Hellich 1877 Arch.natarw.Landes forsch.Bohm 3.

Daphnia venrticosa Hellich 1877 Arch.natarw.Landes forsch.Bohm 3.

Daphnia rosea Hellich 1877 Arch.natarw.Landes forsch,Bohm. 3.

Daphnia aquilina G.O. Sars 1890 Forh, Videnskselsk.Krist. 1.

Daphnia longispina v. littoralis G.O. Sars 1890 Forh. Vidensk Selsk. Krist 1.

Daphnia longispina v. caudata G.O. Sars 1890 Forh.Vidensk Selsk. Krist. 1.

Daphnia longispina v. cavifrons G.O. Sars 1890 Forh.Vidensk.Selsk. Krist. 1.

Daphnia hellichi Stingelin 1895 Rev. suisse. Zool. 3.

Daphnia longispina O.F. Müller. Lilljeborg 1900 Cladocera Sueciae.

Daphnia longispina subsp. longispina O.F.Müller. Rylov 1935. Die Binnengewässer 15.

Daphnia longispina O.F. Müller. Scourfield and Harding 1941. Sci.Publ. Freshw. Biol. Ass. 5.

Daphnia longispina O.F. Müller. Wagler 1937 (partim) Die Tierwelt Mottdemopass 2.

In recent years it has become the practice to re-unite all the numerous described forms of the '*longispina*' group into one comprehensive

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[x] Footnote

No purpose is served by listing all the names that have been given to this and the succeeding species. There are more than a hundred named forms of the *longispina-hyalina* series alone.

species. Refusal to recognize the splinter species of last century is admirable; but the process has gone too far. It is impossible to justify the inclusion of *D. cucullata* in this species and there are good grounds for excluding the '*hyalina*' series. It cannot be doubted that *D. hyalina* represents a series of forms which are distinct morphologically and genetically from *D. longispina*. The distinguishing features of *D. hyalina* are maintained through generations of culture, with sexual reproduction, in conditions more appropriate for *D. longispina*. The much vaunted intermediates are extremely rare, and it is probable that if better diagnostic characters were discovered they would be found to be non-existent. Forms of *D. longispina* and *D. hyalina* can maintain themselves in the same habitat, even when sexual reproduction occurs. Thus on biological grounds, one must admit that there are at least two species in this complex. The fact that it is impossible to differentiate them clearly, except on average characters, is of no importance. Similar species groups are known in other animals (e.g. Geospizidae, Lack 1947); Drosophila and Anopheles, Mayr 1942). It is not unlikely, however, that the accepted boundary between these 'species' is not the true boundary. It is even possible that more than two species are involved. A redefinition should not be undertaken, except after a general study of very many races. For this reason I have adopted the old classification, except as to rank.

Possibly because of the difficulties of definition, most recent authors have treated *D. longispina* and *D. hyalina* as sub-species. This leads in my opinion to an excessively cumbersome nomenclature, since the use of quadrinomials can hardly be avoided. Moreover, it violates the modern conception of the nature of sub-species, as formulated by Mayr (1942) and others. The two series show no clear spatial separation, even on the eco-topographical level, and seem to be reproductively isolated.

For these reasons I prefer to regard D. longispina and D. hyalina as separate species.

In D. longispina the form varies from heavily built to slender. The body may be scarcely compressed or highly compressed. The size range is from 1.0 to 2.5 mm. rarely larger.

The head is usually comparatively large. There is no crest, or at most a very rudimentary one, in the adult. The rostrum is usually large and conspicuous, and has a characteristic shape (Fig. 9a) (The exact shape, of course, varies; but the type of rostrum is constant.). The olfactory setae spring directly from the basal plate of the rostrum, though the antennule is commonly represented by a slight oblique elevation, as in D. curvirostris. A definite antennule mound is lacking.

A pigmented ocellus is almost always present, though it may be unpigmented in exceptional individuals.

The carapace is only moderately clear, and it may be deeply coloured with brown or pink pigment. The carapace reticulations are well marked. The dorsal and ventral carapace margins have numerous long spinules. The carapace spine is usually moderately long, but may be short or very long. It is not normally absent.

The abdominal processes have few or no setae. The first and second may be fused for a short distance at the base. The post-abdomen is of moderate size to large. The dorsal margin is almost straight. The anal denticles, 10 to 16 in number, increase rapidly in size distally. The claws have a more or less well developed denticulation, the denticles being typically divided into three series by two minute gaps. Occasionally the most proximal denticles are slightly stronger than, and slightly set off from, the rest; but there is never a true comb.

The collecting ~~filtratory~~ setae are rather fine and closely set, being about 7.0 to 8.0 μ apart.

This species has a modification, precisely comparable to the '<u>minnehaha</u>' forms of <u>D. pulex</u>. I have seen such specimens from the Lago da Lago, near Cortina d' Am~~b~~pezzo, Italy; and from Little Stanmore Common, Middlesex. There is very little resemblance in ecological conditions between these two habitats.

The species is found throughout the British Isles and is probably our commonest <u>Daphnia</u>. It is found in ponds, slowly flowing waters, and small lakes. I have found a form in a brackish pool in S. Uist (Loch on Mhor).

Abroad it has an almost cosmopolitan distribution, but is commonest in temperate areas. Like <u>D. pulex</u> it occurs in the arctic; but it is less common than that species. In some areas, as the Alps, forms assigned to this species have been found in large deep lakes.

<u>Daphnia hyalina</u> Leydig 1860. Natar geschichte der Daphniden 1860.

Synonyms:- <u>Daphnia lacustris</u> G.O. Sars 1861 Forh. Vidensk Selsk.Krist.

<u>Daphnia galeata</u> G.O. Sars 1863 Indoeretnig tilacad. Coll. v. det Kongl. Frederisk Universitet Christiania p. 21.

<u>Daphnia pellucida</u> P.E. Müller 1867 Danmarks Cladocera.

<u>Daphnia jurassica</u> Barkhardt 1899. Rev. Suisse Zool. <u>7</u>.

Daphnia jardinii T. Scott Rep. Fish. Bd. Scot. **9**.
Hyalodaphnia kahlbergensis Daday. Brady 1898. Nat.Hist.Trans.
Newcastle **13**.
Daphnia hyalina Leydig. Lilljeborg 1900. Cladocera Sweirae.
Daphnia longispina subsp. hyalina Leydig. Rylov 1935.
Die Binnengewasser **15**.
Daphnia longispina O.F. Müller. Wagler 1937 (partim)
Die Tieswelt Mitteleuropas **2**.
Daphnia hyalina Leydig. Scourfield and Harding 1941. freshw. Biol.
Ass. Sci.Publ. Freshw. Biol. Ass. **5**.

For the reasons stated under *D. longispina*, I prefer to treat this as a distinct species. The species is so very variable that it is difficult to give any characters that are at once, definite, distinctive, and present in all forms.

The form is usually graceful and slender. The body is always compressed, usually markedly so. The size without the crest is usually from 1 to 2 mm., but individuals of less than 2 mm. are by far the most common, at least in the British Isles. In my experience seasonal size variations are very marked in this species.

The head without the crest is usually small as compared with *D. longispina*. The rostrum is somewhat variable, but it is never as pronounced or 'beak-like' as in *D. longispina*.

D. hyalina lacustris, at least, is also distinguished by the short oblique antennule mound from which the olfactory setae arise (Fig.9b). This is very idifferent to the arrangement in *D. longispina*, and in my experience is constant. It seems also to be present in all published records where this region is adequately figured.

The eye is usually small with regularly arranged lenses. The ocellus is minute, but not normally absent. A conspicuous crest is always present in the summer, though it varies greatly in size from race to race. In winter the crest may be entirely lost, though this is unusual in England, where a slight crest is commonly retained, and some races show high crests, even in winter.

The carapce is normally very hyaline and colourless. Rarely it may have a deep fuscous pigmentation. I have seen such specimens in S. Uist. The carapace recticulations are faint and often almost absent. The dorsal and ventral carapace margins have numerous long spinules. The carapace spine is normally long, sometimes exceeding the carapace in length.

The ~~filtratory~~ collecting setae are fine and closely set, being 5.0μ to 7.0μ apart.

The post-abdomen is much as in *D. longispina* but smaller and more weakly armed. The denticulation of the claws is less prominent.

An immense number of varieties of this species has been described, but most are obviously invalid. If the differences taken as distinctive of some of these forms were to be accepted, then almost every population would need its own special name. Such a nomenclature would be a cumbrous nuisance. Most of these forms are best ignored. In the British Isles the species falls into three moderately distinct groups, which can be called v. *hyalina*, v. *lacustris*, and v. *galeata*. Scourfield and Harding also recognize v. *pellucida*, but this is not, in my opinion, separable from v. *hyalina*. In Buttermere and Crummockwater both of these forms are found, together with all intermediates.

v. galeata is readily distinguished by its pointed, or sometimes, in winter, angulate, head. The exact size and shape of thehelmet is extremely variable. In extreme cases it may exceed the rest of the body in length. An interesting problem is present by the persistence of such high-helmeted forms throughout the year in some English localities, such as Windermere, whilst in Denmark and in the U.S.A. high crests are not normally found, unless the water temperature exceeds 12° to 16°C.

v. hyalina includes round-headed forms, in which the ventral head margin is straight or nearly straight, or is convex (pellucida.) The crest is commonly fairly high. The carapace reticulations are usually less distinct than in lacustris.

v. lacustris can be taken to include forms in which the vental head marginis distinctly concave, the crest is usually low and the carapace reticulations are usually well marked.

v. galeata is sharply set off from the other two types, but it is not easy to decide whether or no theres is a valid distinction between hyalina and lacustris. I have on several occasions found individuals of a 'lacustris' population with a 'hyalina' head shape, though agreeing with 'lacustris' in other features. It is convenient to regard the two races as distinct, since they appear to have different ecological requirements in the British Isles. D. hyalina when found in small waters is nearly always of 'lacustris' type, whilst hyalina is dominant in larger waters. The occurence of exceptions indicates that the difference is not merely phenotypic.

This species also shows a 'minnehaha' variation. The form was first described from the Juras as D. jurassica. Gurney (1923) notes that he has found such individuals in Esthwaite water. I have found them in Windermere at Borran's field, in a clear space in the reed-beds. It is noteworthy that the animals concerned were all round-headed, though in Windermere the dominant form is v. *galeata*.

The species as a whole is very widely distributed and common in the British Isles. It is found in most lakes and many large ponds. It is rare, but not unknown in small ponds.

Abroad it has a circumpolar distribution, being most abundant in cool temperate and montane regions. It does not extend into the Arctic. Several racial types are limited either to Europe or America. In many areas, as on the central plain of Europe, the species is much less common than in the British Isles, being largely restricted to large deep lakes.

Daphnia cucullata G.O. Sars 1861 Forh. Vidensk. Selsk. Krist.

Synonyms:- *Daphnia jardinii* Baird 1857 Edinb.New.Philosph.Journ.New Ser. **6**.
Hyalodaphnia kahlbergensis Schödler 1866 Arch.Naturgesch. 32.
Hyalodaphnia cucullata Schödler 1866.Arch.Naturgesch. 32.
Hyalodaphnia berolinensis Schödler 1866 Arch.Naturgesch.32.
Daphnia apicata Kurz 1874 Arch.naturw.Landes Forsch.Böhm 3.
Daphnia berolinensis Eylmann 1886 Ber.naturt.Ges.Freiburgi(1) **2**.
Daphnia hermanni Daday 1888 Crustacea Cladocera Faunae Hungaricae.
Hyalodaphnia jardinii (G.O. Sars). Brady 1898 Nat.Hist.Trans. Newcastle **13**.

Daphnia (Hyalodaphnia) cucullata G.O. Sars. Lilljeborg 1900.
Cladocera Sueciae.
Daphnia cucullata G.O. Sars. Rylov 1935 Die Binnengeirässer 13.
Daphnia cucullata G.O. Sars. Scourfield and Harding 1941
Sci.Publ.Freshw. Biol.Ass. 3.

With *D. ambigua* this is the smallest British species. Individuals may reach 2 mm., without the crest, but one mm. is a more usual size. The form is usually somewhat slender; and typically highly compressed.

The head has always a crest, at least in summer, and this is typically very long and pointed. The ventral head margin is almost straight. The rostrum is short and blunt. The antennules are vestigial, the olfactory setae arising directly from the rostrum, almost at its apex. The eye is small, with regularly arranged lenses. The ocellus is normally invisible and without pigment, very rarely, it may be pigmented in a few individuals.

The carapace is very hyaline. The reticulations are indistinct. The dorsal and ventral margins have a number of slender spinules. The carapace spine is always well developed.

The post-abdomen is small. The anal denticles are weak and few in number (usually 6 to 10.)

The species is variable, though less so than *D. hyalina*. At the present time it is pointless to distinguish the numerous named 'varieties.' Following Wagler (1933) a distinction can be drawn between permanently roundheaded forms (v. *hermanni*), in which the crest is always low; and forms with a more or less pointed crest in summer, in which the crest may be very high indeed. Both occur in England. Here forms with rounded head are not uncommon, but forms with high helmets are comparatively rare.

The species is nowhere common in this country; it is widely distributed but most often found in the S. and E. Here it is usually found in ponds and very small lakes.

Abroad it is confined to the palaearctic region; but is absent from the most northerly areas. In most of its range it is a characteristic lake species, though less definitely lacustrine than *D. hyalina*.

The following key may be of use in identifying males.

1 (4) (~~a~~) Lateral seta terminal, between flagellum and olfactory setae (Figs. 1d, 3c.) 2

(~~b~~) Flagellum nearly straight terminal portion with long setae(Figs. 1d, 3c.)

2 (3) (~~a~~) Flagellum longer (Fig. 3c.) *D.atkinsoni*

(~~b~~) Papillae bearing openings of vasa deferentia small and unarmed (Fig. 2c.)

3 (2) (~~a~~) Flagellum shorter (Fig. 1d) *D. magna*

(~~b~~) Post-abdomen with a marked dorsal inflation distally which bears numerous small spines, and on which the sperm-duct opens.(Fig.1c.)

4 (1) (~~a~~) Lateral seta not terminal, flagellum between this and olfactory setae (Figs.10a,10b,10c,10d,10f). 5

(~~b~~) Flagellum distinctly curved, terminal portion never with long setae (Figs. 10a,10b,10c,10d,10f.)

5(12) Flagellum distinctly longer than olfactory setae 6

6 (7) (~~a~~) Thickened portion of flagellum inflated in middle of its length (Fig. 10d.) *D.ambigua*

(~~b~~) Characteristic 'spoon-shaped' tip to flagellum (Fig. 10e.)

7 (6) (~~a~~) Thickened portion of flagellum of uniform width or tapering (Figs. 10a, 10b, 10c, 10f). 8

(~~b~~) Tip of flagellum not of this form

8 (9) (~~a~~) Falgellum very long, over 5 x length of longest olfactory seta (Fig. 10b). D. curvirostris

(~~b~~) Lateral seta inserted on a level with olfactory setae.

9 (8) (~~a~~) Flagellum normally less than 5 x length of longest olfactory seta. 10

(~~b~~) Lateral seta inserted proximal to olfactory setae.

10(11)(~~a~~) Flagellum normally 3 to 4.5 times length of longest olfactory seta (Fig. 10a). D. obtusa

(~~b~~) 2nd abdominal process not very large; not or not markedly projecting beyond carapce valves.

11(10)(~~a~~) Flagellum normally 2 to 3 times length of longest olfactory seta (Fig.10c.) D.pulex

(~~b~~) 2nd abdominal process very large, projecting markedly beyond carapce valves.

12(5) Flagellum little if any longer than longest olfactory seta. (Fig. 10f). D.longispina, D.hyalina, D.cucullata.

Description of Figures.

Fig. 1 (a) *Daphnia magna* ♀ which has previously been ephippiate, Hampton Water Works 25.11.48.

(b) *Daphnia magna* ♀ dorsal view of head, Wellcome Institute culture 2/51.

(c) *Daphnia magna* ♂ post-abdomen of adult

(d) *Daphnia magna* ♂ antennule of adult

Fig. 2 (a) *Daphnia atkinsoni* ♀ ephippial, Berrylands, Surrey 3/50.

(b) *Daphnia atkinsoni* ♀ post-abdomen, Berrylands, Surrey 3/50.

(c) *Daphnia atkinsoni* ♂ ventral view, Berrylands, Surrey, 3/50.

Fig. 3 (a) *Daphnia atkinsoni* ♀ head, Berrylands, Surrey 18.1.50.

(b) *Daphnia atkinsoni* ♀ claw, Berrylands, Surrey 18.1.50.

~~(c) *Daphnia atkinsoni* antennule.~~

~~Fig. 4 (a) *Daphnia pulex* head~~

~~(b) *Daphnia pulex* dorsal portion crest of young individual of *minnehaha* type, Fowlmere, Norfolk 10.7.48.~~

~~(c) *Daphnia curvirostris* head.~~

Fig. 5 (a) *Daphnia pulex* ♀ end of post-abdomen, Leg of Mutton Pond, Hampstead Heath 10/50.

(b) *Daphnia curvirostris* ♀ end of post-abdomen, Botany Garden, Bedford College 10/50.

(c) *Daphnia obtusa* ♀ end of post-abdomen, Botany Garden, Bedford College 10/50.

Fig. 6 (a) *Daphnia curvirostris* ♂ Botany Garden, Bedford College 17.11.50.

(b) *Daphnia curvirostris* ♂ post-abdomen, Botany Garden, Bedford College 17.11.50.

(c) *Daphnia obtusa* ♂ culture from Newdigate, Surrey 11/50

Fig. 7 (a) *Daphnia obtusa* ♀ head, Botany Garden, Bedford College 16.1.50.

(b) *Daphnia obtusa* ♀ rostral region, culture from Newdigate, Surrey, 11/50.

(c) *Daphnia obtusa* ♀ ventral carapace margin, culture from Newdigate, Surrey 11/50.

Fig. 8 (a) *Daphnia ambigua* ♀ young, culture from Queen Mary's Garden, Regent's Park 10/50.

(b) *Daphnia ambigua* ♀ head, culture from Queen Mary's Garden, Regent's Park 10/50.

(c) *Daphnia ambigua* ♀ rostral region, culture from Queen Mary's Garden, Regent's Park 10/50.

(d) *Daphnia ambigua* ♀ abdominal processes, culture from Queen Mary's Garden, Regent's Park 10/50.

Fig. 9 (a) *Daphnia longispina* ♀ head, Clare Brook 26.7.48.

(b) *Daphnia hyalina v. lacustris* ♀ head of winter form, culture from Regent's Park Lake 10/50.

Fig.10 (a) *Daphnia obtusa* ♂ antennule, culture from Newdigate, Surrey 11/50.

(b) *Daphnia curvirostris* ♂ antennule, Botany Garden, Bedford College 17/11/50.

(c) *Daphnia pulex* ♂ antennule, after Scourfield.

(d) *Daphnia ambigua* ♂ antennule, after Scourfield.

(e) *Daphnia ambigua* ♂ tip of flagellum, after Scourfield.

(f) *Daphnia longispina* ♂ antennule, after Lilljeborg.

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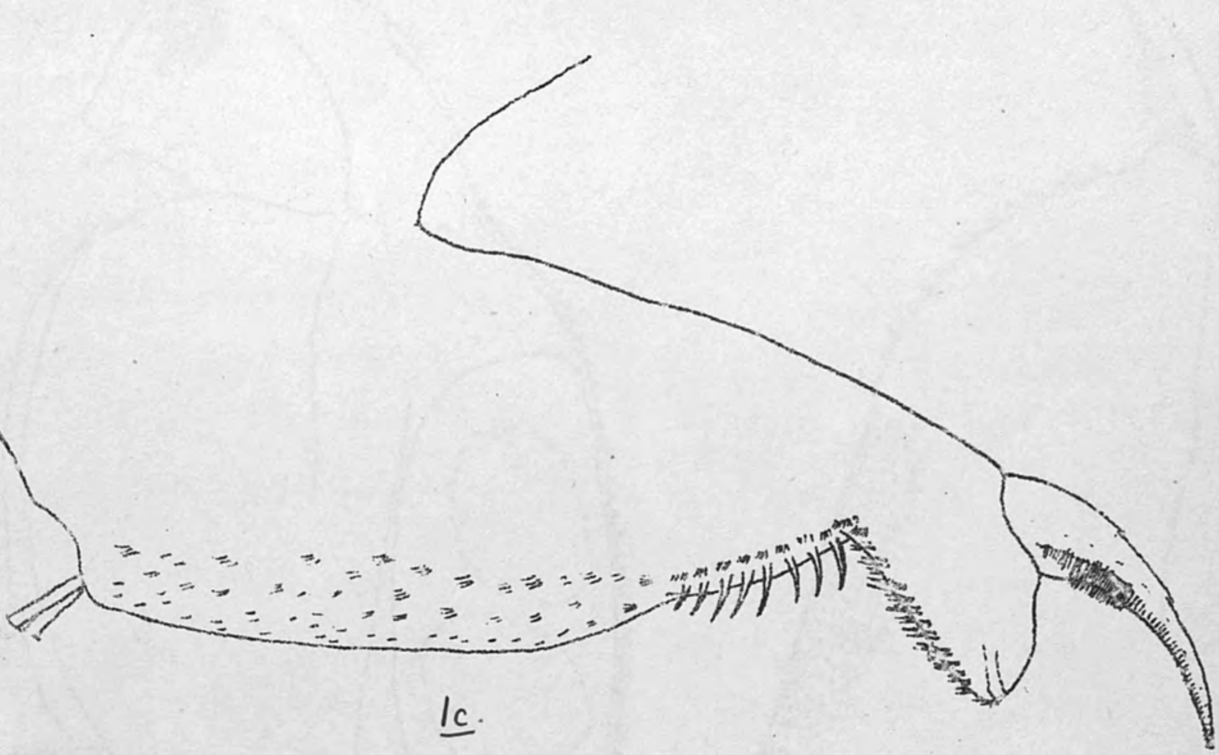
The males of *Daphnia*:-

As with most genera of Cladocera the males of this genus are usually ignored in systematic accounts, and in differentiating species. The justification for this has been the rarity with which males are encountered. At the present day it is easy to produce males of most species of *Daphnia* in the laboratory (except in the case of the exceptional thelytokous races), and thus they can be used successfully in determining species. It is well-known that in the genus *Moina* the males are often more distinctive than the females. My experience indicates that this is also true of the genus Daphnia, though to a more limited extent. For purposes of identification the most useful structure appears to be the antennule, which shows comparatively little intra-specific variation, but varies conspicuously from species to species.

The characters of the males ought also to be taken into account in assessing the inter-relations of the species. In my opinion, for instance, the widely divergent males of *D. ambigua* and *D. longispina*, make it impossible to concur with Scourfield's suggestion that the former is derived from the latter.

It may be noted that the structure of the male antennule seems to confirm the validity of the two sub-genera, based as they are mainly on female characters. Thus *D. magna* and *D. atkinsoni* agree with each other and differ from the species of *Daphnia* s.s. in the position of the lateral setae and the general structure of the flagellum.

I wish to express my thanks to Professor Munro Fox, who has assisted in many ways, and to all members of this Department who have given time to follow and criticize my views, and also to Dr. J.P. Harding for his very willing advice and criticisms.



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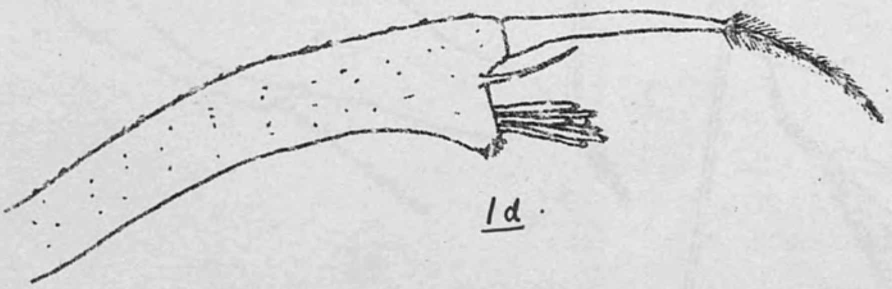

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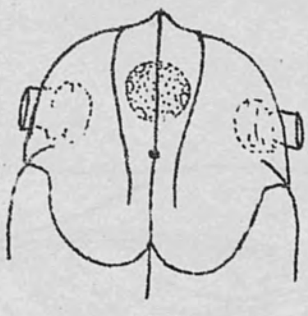

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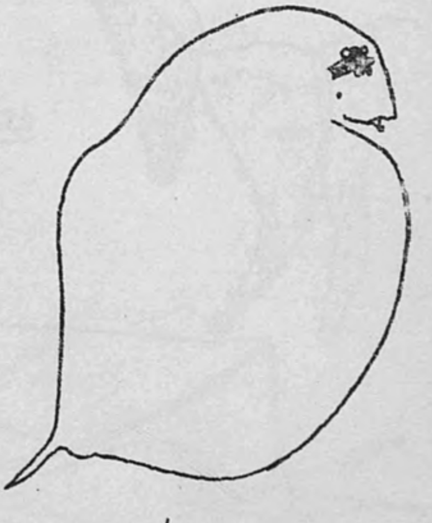

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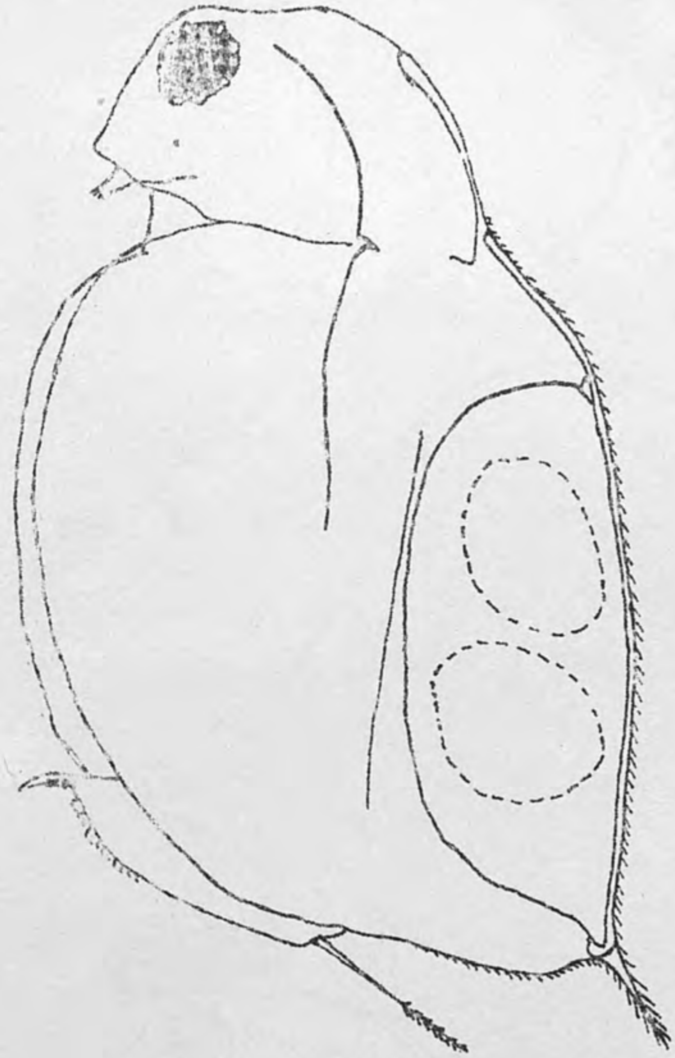

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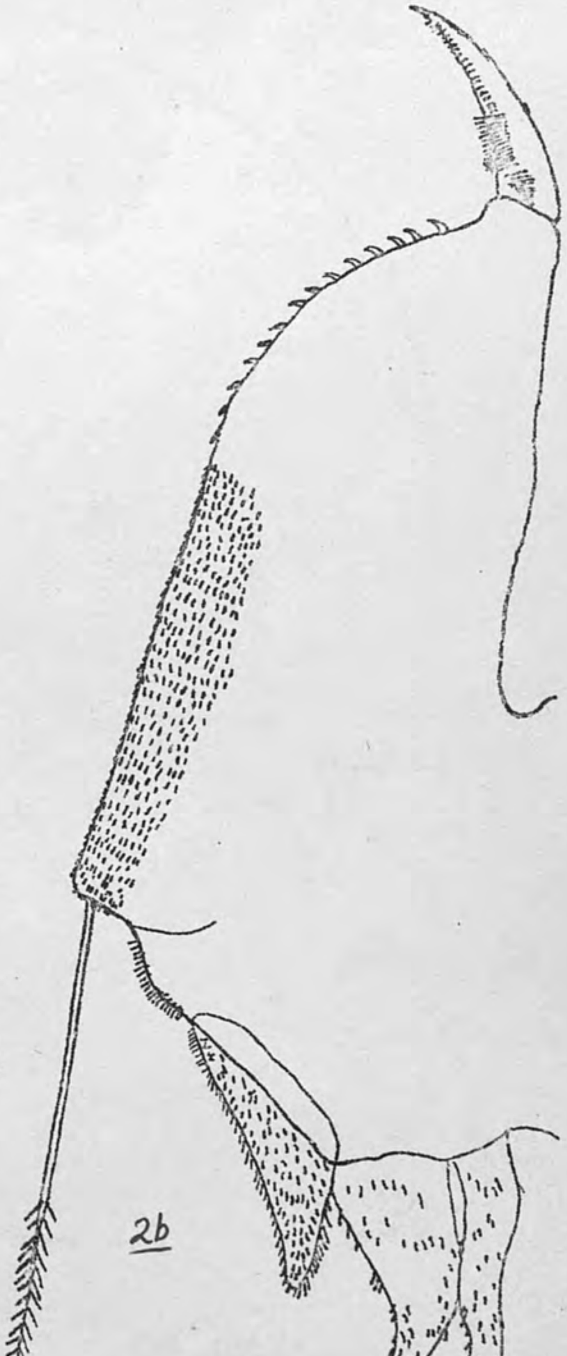

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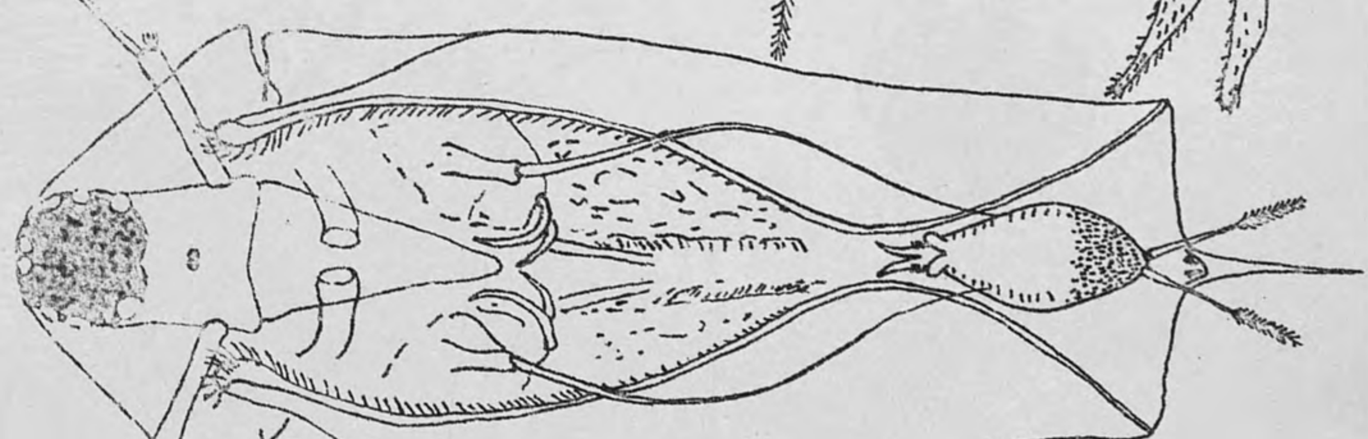

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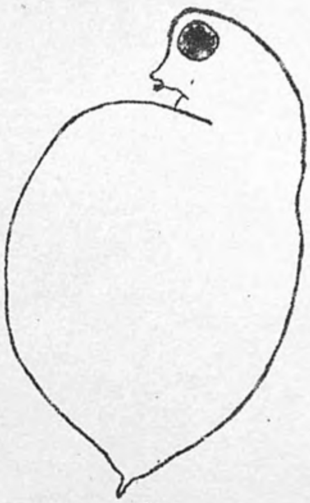

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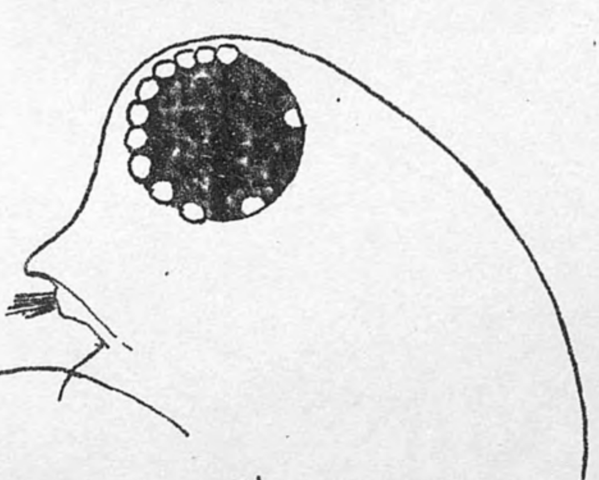

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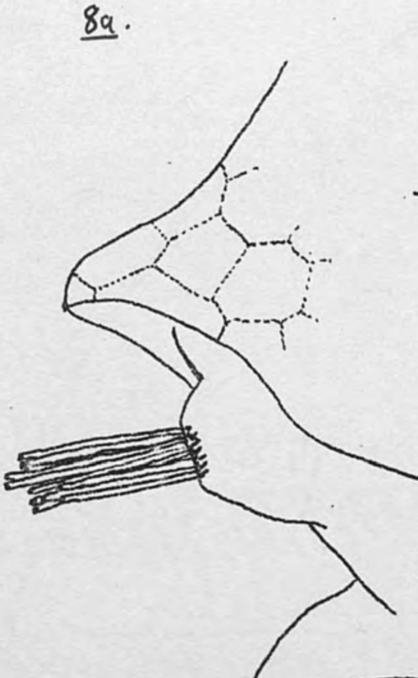

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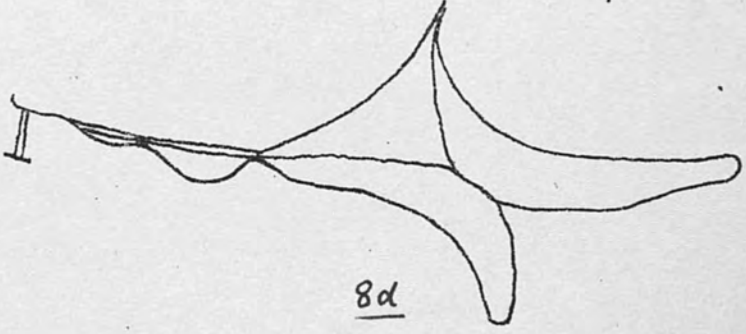

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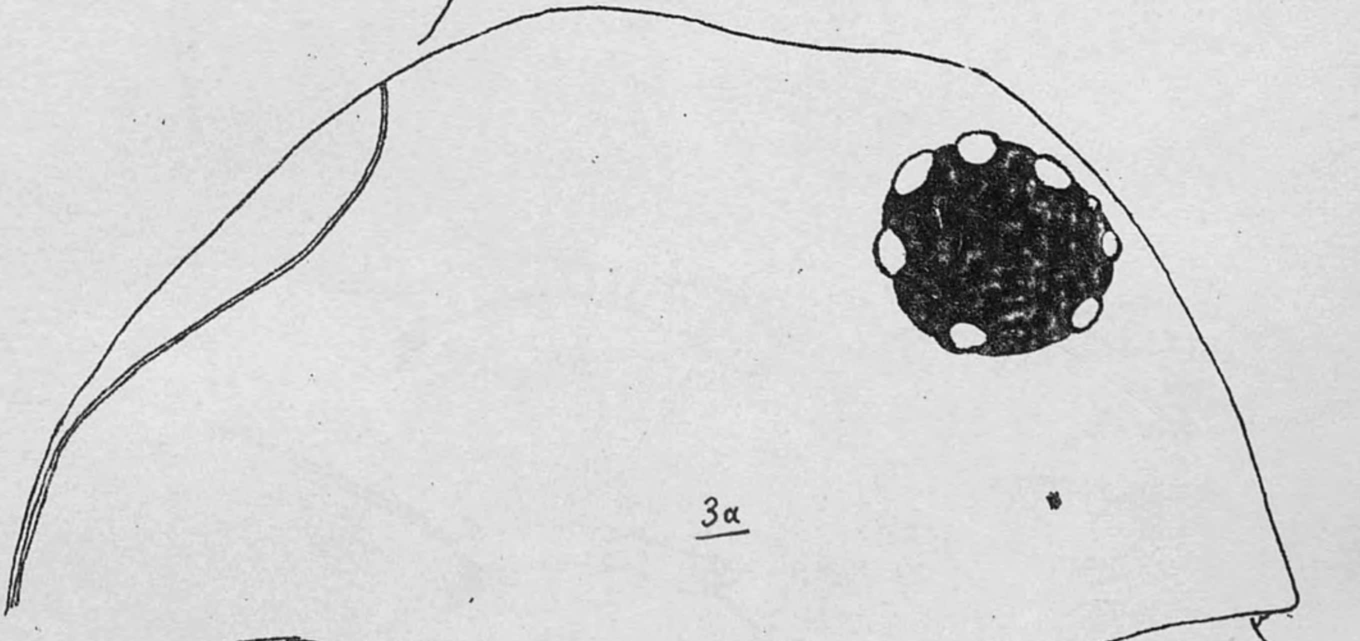

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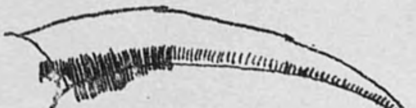

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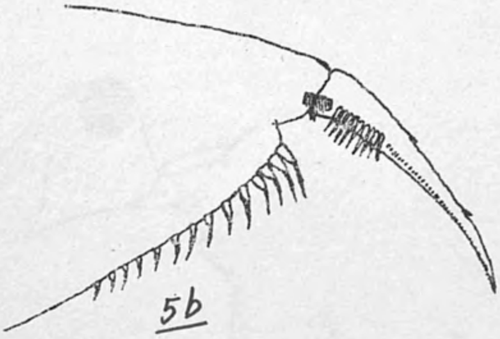

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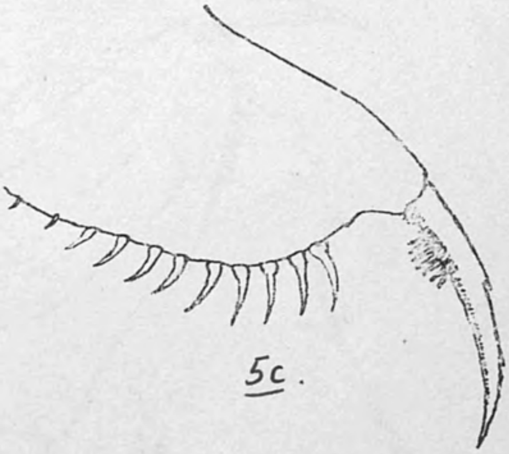

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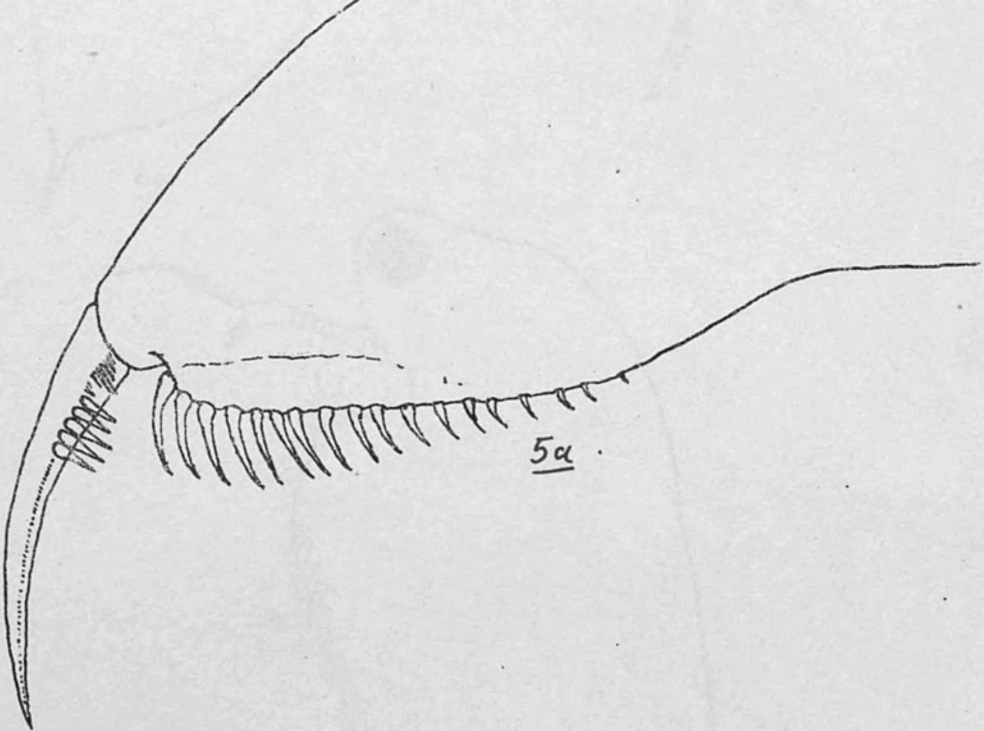

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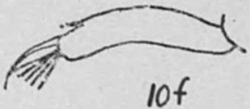

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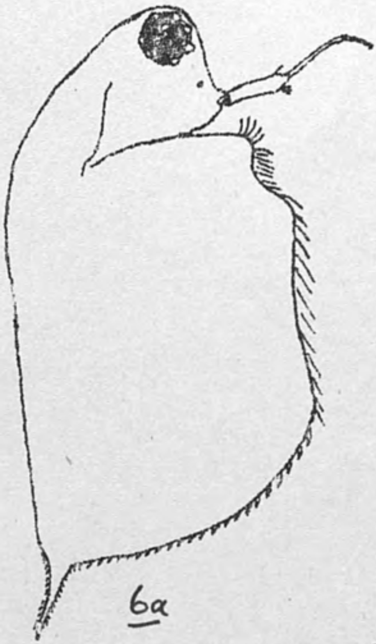

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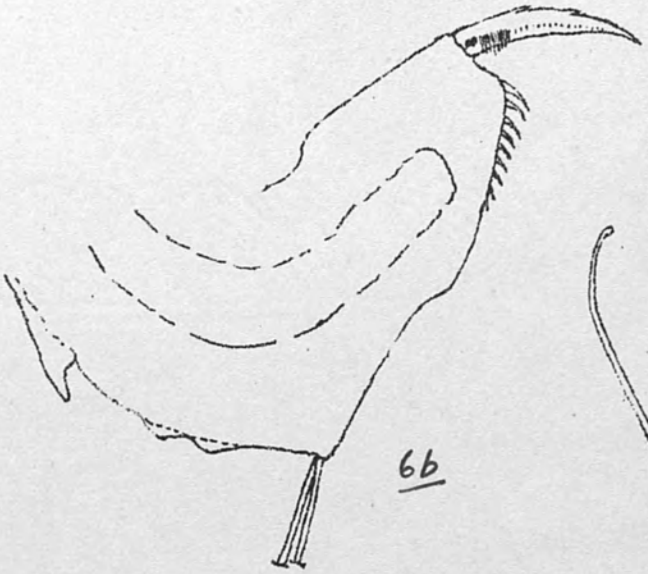

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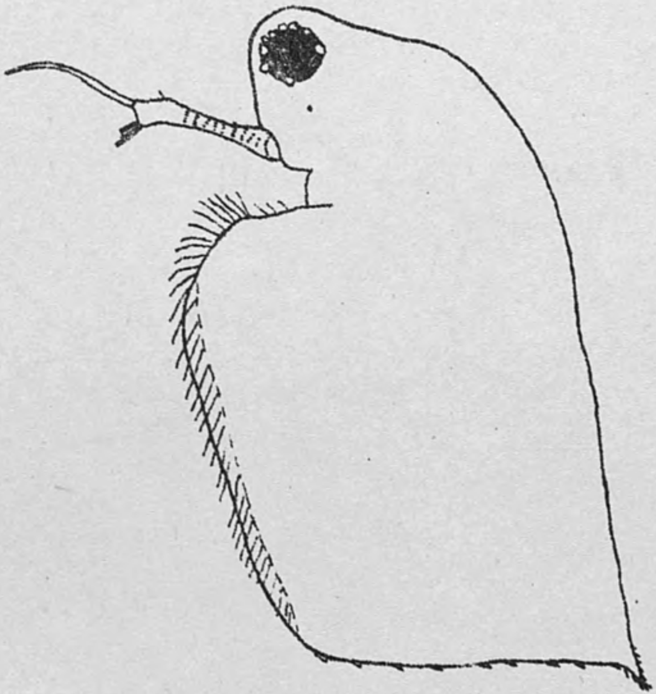

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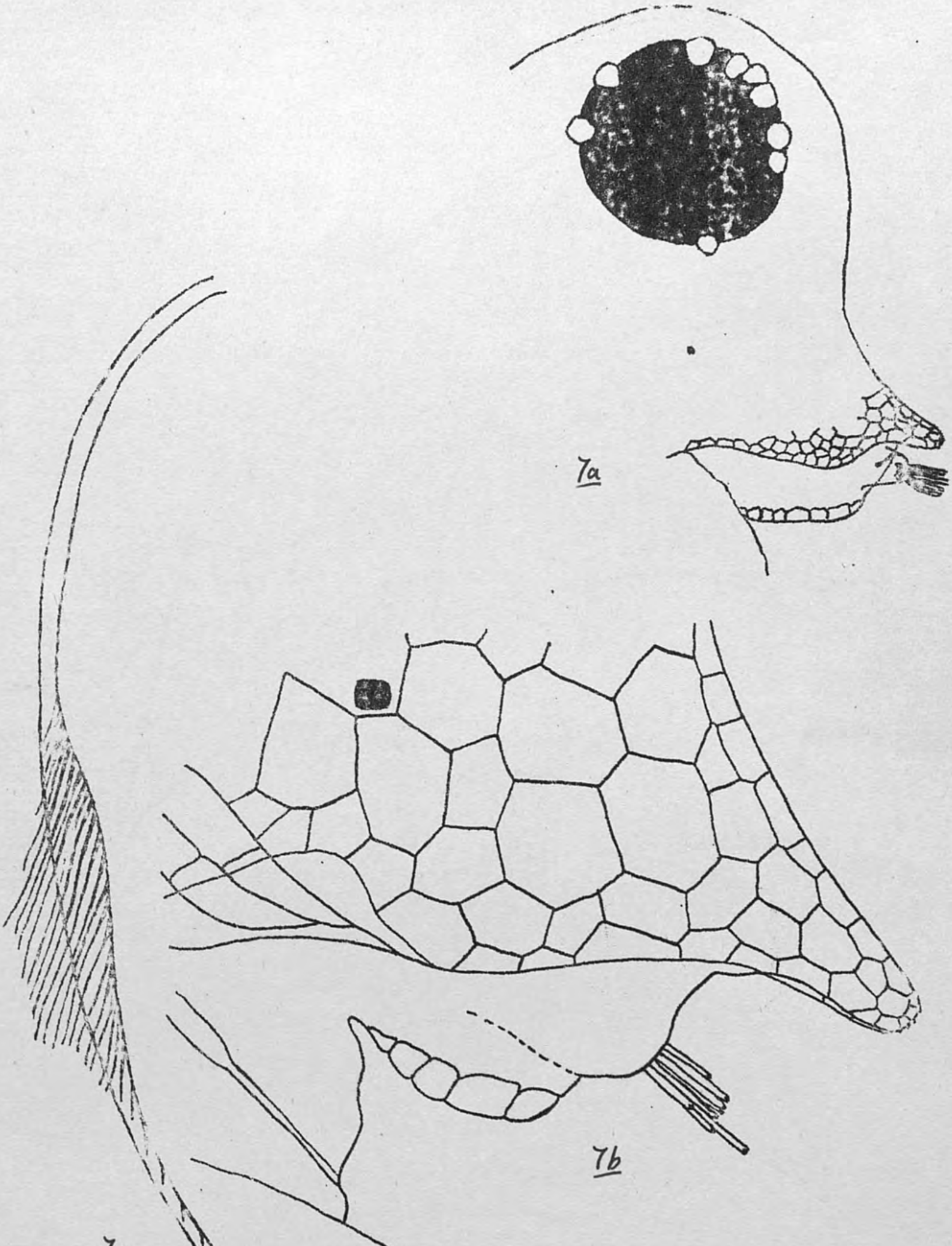
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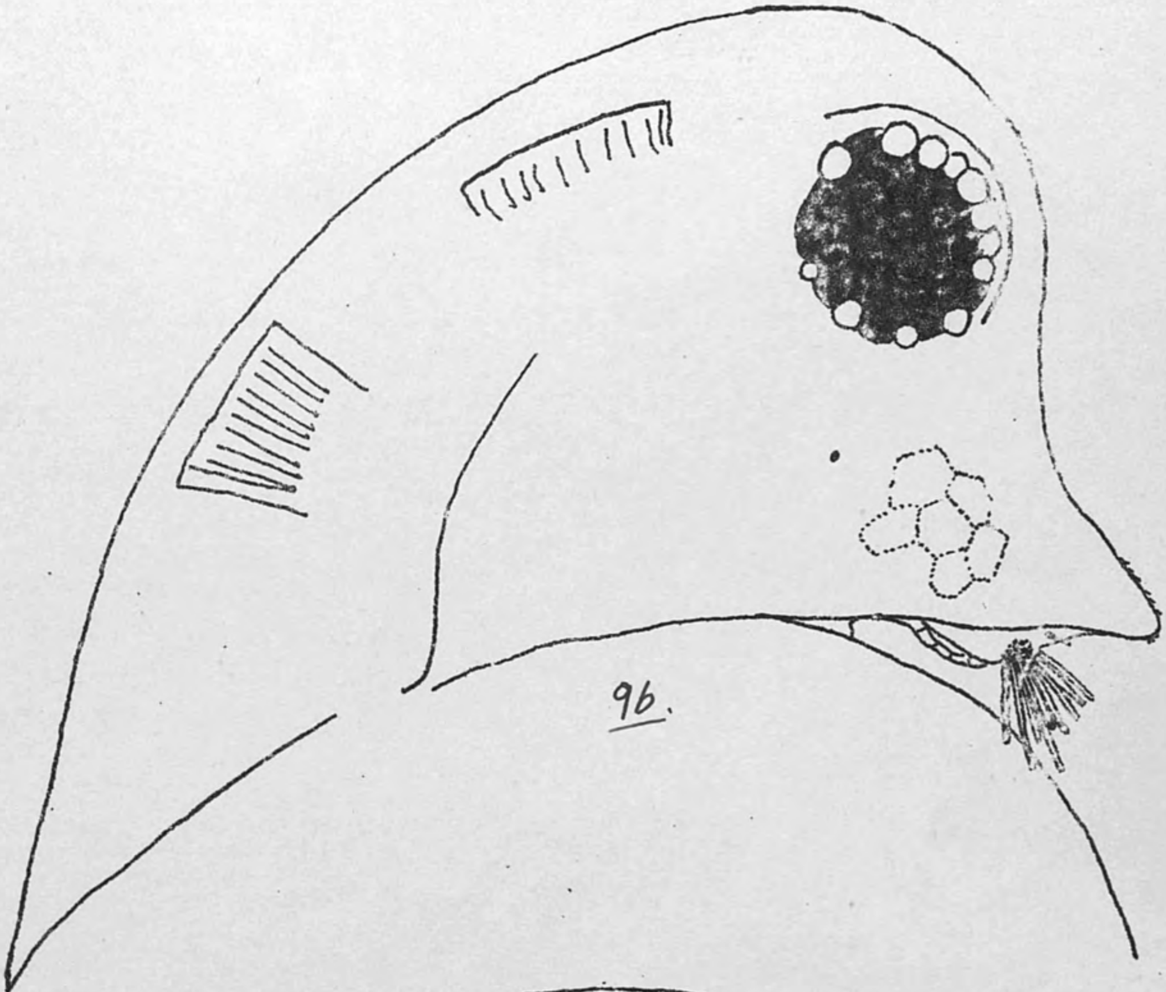

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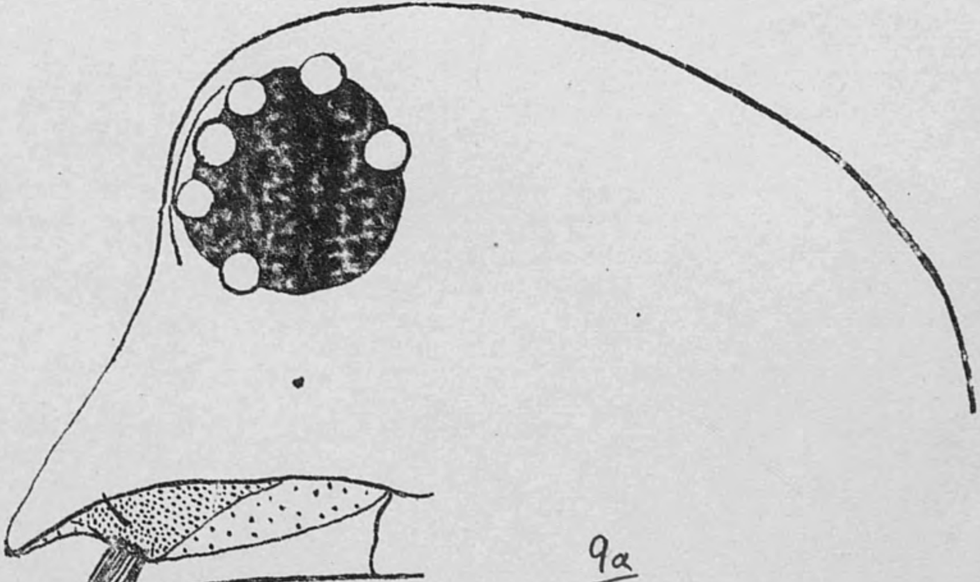

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