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STUDIES ON CONNECTICUT LAKE SEDIMENTS.

III. THE BIOSTRATONOMY OF LINSLEY POND.

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ABSTRACT. Counts of animal microfossils per cubic centimeter of wet sediment are reported for three borings in the bottom of Linsley Pond, North Branford, Connecticut. Comparisons are made with similar "fossils"

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in recent deposits of the same lake and of other Connecticut lakes. The ancient sediments have been dated by pollen-analysis (Deevey 1939).

The general sequence of numbers follows the curves for organic matter, with an exponential rise, a period of more or less stable equilibrium, and a decline which is probably due to changes within historic times. This type of curve of development is particularly well exhibited by *Bosmina*; the relation of numbers of *Bosmina* to total organic matter obeys the equation of allometric growth, $y = bx^k$. *Bosmina longirostris* succeeded *B. coregoni longispina* early in the deciduous forest period, at the time of maximum organic matter. Six other species of cladocera have been recognized as microfossils.

The numbers of heads of chironomid larvae follow a similar curve, except that in two borings a pronounced maximum of *Tanytarsus* corresponds with the earliest (spruce-fir) period. Presumably this is because the silty sediments of this period accumulated much more slowly than the later deposits. Qualitatively the chironomid fauna since the *Tanytarsus* maximum has been very diverse, but the sequence is essentially in conformity with that expected with increasing eutrophication and a declining oxygen supply in the hypolimnion. The mesotrophic subgenera *Endochironomus* and *Glyptotendipes* were followed by *Chironomus sens. str.*

Fragments of *Chaoborus* larvae are found in sediments from very early levels, but their maximum falls in the middle part of the deciduous forest period (oak-hickory).

The statoblasts of *Plumatella repens* rose to a maximum at the time of maximum organic matter, and then declined. The decline is taken to indicate a decrease in the available substratum, and thus a restriction of the zone of littoral vegetation, probably through shading by phytoplankton. The occurrence of a statoblast of the warm-water stenotherm *Pectinatella magnifica* in deposits of the spruce-fir period indicates that the summer surface temperature of the lake rapidly rose to 18° or 20° C.

Stems and leaves of *Fontinalis* occur in samples of the silty, *Tanytarsus*-rich sediments of the earliest spruce-fir period. If this moss grew *in situ* at 14.5 meters, the transparency of the lake at that time was much greater than today.

Other microfossils were found but apparently they lack typological meaning. The most significant features of the development of the lake are summarized in Text Fig. 7. Studies by other workers, as well as the present investigation, indicate that the normal course of lake succession is from "oligotrophy" to "eutrophy," but it is difficult to disentangle the effect of simple reduction of mean depth (morphometric eutrophication) from that of an increased supply of nutrients (edaphic eutrophication) or the even more problematic effect of climate.

An attempt is made to estimate the length of time represented by the deposits of Linsley Pond on the basis of the number of *Bosmina* living in the modern lake, the loss of carapaces to the sediment, and the number found as fossils. This attempt is greatly hampered by the lack of relevant information about living *Bosmina* and their rate of production, but the highly speculative calculation yields as its most probable result the reasonable figure of 11,300 years.

Appendix I, by Thomas S. Austin, confirms the identification of the fossil species of *Bosmina*, and discusses their distribution in modern Connecticut lakes. Dr. Minna Jewell reports on sponge spicules in Appendix 2, and in Appendix 3 Prof. G. E. Hutchinson describes a fragment of the aquatic hemipteran *Buena elegans* from the sediments of Lyd Hyt Pond.

INTRODUCTION.

STATEMENT OF PROBLEMS.

THE study of the succession of lake types has occupied the author's attention for nearly six years. During this time several preliminary and subsidiary research problems have been attacked and the results have been published (Deevey 1939, 1940, 1941a, 1941b), but although Hutchinson and Wollack (1940) have described chemical analyses that strike at the heart of the matter, this is the first paper from the present author to be unequivocally directed toward the main project. A brief statement of the aims of this work should therefore not be out of place.

As the viewpoint from the beginning has been that of the general limnologist, limnological problems will first be discussed, but it is recognized that the solution of these is not the only, or perhaps even the most important, justification for biostratonomy.¹

The classification of modern lakes, involving as it does the analysis of their biocoenoses and metabolism, is analogous to comparative morphology and taxonomy on the "organismic" level. Now, while it is axiomatic that the present is the key to the past, the embryologist knows that the converse is equally true, and that many features of the adult organism are unintelligible without information about the past history of development. One need not be a holist or an emergent evolutionist to grant that a knowledge of the development of the "superorganism" is equally essential to a full understanding of the mature biocoenosis.

Some examples may serve to illustrate this generalization. In Linsley Pond Riley (1940) has shown that the standing crop of phytoplankton is greatly in excess of that of zooplankton, the P:Z ratio lying between 4.5 and 9.4, depending on the method of estimate. The very slight evidence available indicates that this is, at the least, an unusual phenomenon. A careful and extensive study of the development of modern lakes should make clear whether or not this condition is characteristic of a certain stage of eutrophy or senescence, or whether it is associated with cultural modification. Similar considerations apply

¹ In the use of this term the author follows Weigelt (1927) and Wasmund (1929) in thus designating "the mechanical relation of fossil remains to each other and to the sediment."

to the qualitative composition of the bottom fauna. The Connecticut lake types characterized by *Tanytarsus* and "mesotrophic *Chironomus*" (Deevey 1941b) are virtually indistinguishable by oxidation-reduction potential measurements, as well as by more ordinary criteria, and the conclusion was reached that these types have differentiated "by accident." The nature of this accident should be revealed by stratigraphic studies.

A rather more fundamental problem, also amenable to the developmental approach, is posed by Riley's (1940) statistical demonstration that the production of organic matter in Linsley Pond is independent of the standing crop of phytoplankton. Since it is obvious that in the limiting case a standing crop of zero would have zero production, one must expect a positive correlation over part of the range of variation of plankton. In other words, at some time during the history of the lake an irrelation sets in, and a further increase in plankton merely reduces the penetration of light, without increasing the amount of organic matter produced. Evidence bearing on this relationship is drawn from microfossils in a later section.

The analogy between embryogeny and lake development can easily be overstrained, but it is useful in clarifying the phraseology of another vital question: is development determinate or indeterminate? Given sufficient time and an adequate supply of nutrients, do lakes proceed inevitably from oligotrophy to eutrophy, or can the process be modified or even reversed by external circumstances, climate, for example? This is the paleolimnological aspect of the discussion by Strøm (1930), Rawson (1939), and others, of the relative importance of climatic, edaphic, and morphometric factors in the metabolism of lakes. The origin of dystrophy is directly related to this problem. Consideration of another "embryological" question, the effect of changing temperature on rate of development, must await an absolute chronology.

Other limnological matters, such as the chemical dynamics of succession and the typological equilibrium, have drawn the attention of Hutchinson and Wollack, and need not be discussed here. The examples cited by no means exhaust the possibilities, but they should serve to indicate the central part stratigraphy must play in the progress of general limnology. The other aims of biostratonomy may be roughly grouped as geologic and zoögeographic.

The geologic purpose in view is that of all sedimentary studies, namely, to understand the conditions obtaining during and leading to deposition, in order that the information may be applied to the interpretation of ancient environments. Lacustrine sediments from a relatively small but important fraction of the geologic column, and the work of Bradley (1931), on the Green River formation, is an outstanding example of the geologic importance of limnology. The biostratonomy of lakes is especially valuable to Pleistocene research, since most of the known lake deposits are of either post-glacial or interglacial date. One particularly significant contribution of paleolimnology to glacial geology may be the derivation of an absolute chronology on the basis of quantitative counts of microfossils, as outlined in a later section.

The zoögeographic results anticipated from the study of animal microfossils in lake sediments are so obvious as to need little comment. The present geographic distribution of animals is explicable only in the light of past climatic and physiographic conditions, and at least in theory every Pleistocene or post-glacial fossil specifically identified from a known stratigraphic horizon increases our understanding, not only of the modern range of the species, but of the circumstances responsible for its former distribution. The eagerness with which alert zoögeographers seize on bits of fossil evidence is described by Hubbs (1940). Progress in this field must inevitably be slow and is moreover hampered by inadequate knowledge of present ranges, but it should soon become more rapid with the realization that lake sediments are veritable storehouses of freshwater organisms in an excellent state of preservation.

NOMENCLATURE.

In the first paper of this series the author (1939) described the typical organic deposit of Linsley Pond and other small southern Connecticut lakes, compared it to the "gyttja" of European investigators, and proposed that "ooze" be adopted as an English translation of this term. Discussions at the 1938 meeting of the Limnological Society of America and at the Symposium on Hydrobiology held at Madison, Wisconsin in 1940 have shown strong disagreement as to nomenclature among students of recent lake sediments, and "ooze" has not found general favor, except in its usual non-technical sense.

A surprising amount of support for the international terms "gyttja" and "dy" appeared, however, and in a recent paper Lindeman (1941) advocated the provisional adoption, not only of these terms, but of such others as "förna," "ävja," and "sapropel," as defined by Wasmund (1930). In the author's opinion too little is known of the chemistry, structure, and genesis of lake deposits to justify the use of elaborate systems of terminology, which may be useful to specialists but which mislead the uncritical. The available evidence indicates that "sludge" (Twenhofel and collaborators), "ooze" (author), and "gyttja" are synonymous, and as the first is preoccupied, and the second too general, the author agrees with Lindeman in urging the adoption of "gyttja." To do so appears especially expedient at this time, in view of the fact that European workers have reached substantial agreement on the nomenclature of lake sediments (Wasmund 1938, Potonié 1938). In the present state of our knowledge, however, it is imperative, as Lindeman points out, that each term be accompanied by as full a description as the user's information permits.

ACKNOWLEDGMENTS.

This work was begun in 1935 at the suggestion of Prof. G. E. Hutchinson, and in 1938 a study of one Linsley Pond boring (L-2) was described in a Ph.D. dissertation presented to the Graduate School, Yale University, entitled "Typological Succession in Connecticut Lakes." Except for the collection of materials, however, all work reported in this paper was done at The Rice Institute, including the re-examination of boring L-2. It is a pleasure to acknowledge the invaluable guidance of Professor Hutchinson, whose interest in the problem has not abated since the author left the Osborn Zoological Laboratory. Dr. Gordon Riley and Mr. Thomas Austin, of Yale University, have generously made available their data on the plankton of Linsley Pond, and Mrs. Georgiana Baxter Deevey has given assistance with some of the drawings.

METHODS.

The borings were made from the ice by means of the U. S. G. S. modification of the Davis peat sampler. This instrument is generally satisfactory for work on small, shallow lakes,

but great difficulty was experienced in the deep water (13 meters) overlying boring L-10, due to the bending of the rod. Moreover it is impossible to obtain a Davis sample of the unconsolidated sediment above the two-foot level, and all modern samples, including those from other Connecticut lakes, have been secured with the Ekman dredge. The exact stratigraphic position of such modern samples can therefore not be determined, although they are not deeper than 15 centimeters. The samples were stored in shell vials without preservative.

The volume of sediment was measured by displacement of water in a truncated 50-cc. burette, duplicate samples being taken for dry weight and for microfossil analysis. This method is not so accurate as was at first believed, the mean discrepancy between 24 pairs of duplicate determinations of the dry weight of 1 cc. being 7.41 per cent. It is in some respects preferable to the method used by Miss Wollack, that of direct measurement by forcing sediment into a burette, since it avoids the difficulty of compressing very liquid samples and the resulting formation of bubbles. It is probably less accurate for very dry inorganic samples, due to colloidal imbibition. In any case, it is impossible to obtain the dry weight and the microfossil content of the same fraction, and as some variation within the sediments must be expected, the volumes are probably as accurate as is practicable with such small amounts. The discrepancy between the dry weight of 1 cc. of sediment given for boring L-10 in Table 1 and the figures given by Hutchinson and Wollack is due to the drying of the samples in the interim. It is regrettable that the corks were not coated with a waterproof substance, but except in the case of boring L-2, which was collected in 1936, the drying has not been excessive or noticeably uneven, and as the critical comparisons are made on the basis of dry weight, this is not a factor of great consequence.

Dry weights were determined after 36 hours at 110° C.; samples were ignited in the Bunsen flame. As the calcium content of the Linsley sediments is very low, no correction has been applied for loss of CO₂ in determining the organic matter by ignition.

Microfossil counts were made in two ways. The original sample (usually 1 cc.) was diluted with water in removing it from the burette, an equal volume of ten per cent KOH was added, and the sample boiled for a few minutes, in order to break up the larger lumps of sediment and free the microfossils.

The material was then allowed to settle, the excess KOH was drawn off, and the sediment was washed and diluted to a known volume (usually 30 cc.). After thorough stirring had brought all the sediment into suspension, 0.05 cc. was quickly drawn off with a pipette and mounted on a microscope slide. By passing the entire slide under the compound microscope with the aid of a mechanical stage, very small fossils (principally *Bosmina*) could be counted. Four such "micro-counts" were made on each sample, and the results averaged. The deviation between individual *Bosmina* counts made in this way was remarkably small, being frequently less than five per cent when *Bosmina* was abundant, although considerably greater when only one or two fossil *Bosmina* occurred on each slide.

The remaining suspension of sample and water, not significantly depleted by the removal of 0.2 cc., was examined, a fraction at a time, in a petri dish under the highest available power (20 \times) of the binocular dissecting microscope. The dish was ruled with parallel guide lines to prevent omission of any area, and microfossils were removed as they were counted. In this way the larger, less abundant fossils, such as chironomid heads, *Plumatella* statoblasts, *Chaoborus* fragments, etc., were enumerated.

It is probable that by the method adopted a certain class of microfossils, too small to be completely counted under the dissecting microscope and too rare to be reliably estimated under the compound microscope, was overlooked. The list of recognizable microfossils known to be included in this category includes the suctorian cysts, carapaces of cladocera other than *Bosmina*, and rotifer and gastrotrich eggs.

Occasionally one of the larger, less abundant types was encountered in the micro-counts. In this case the occurrence was regarded as accidental, and the fossil was reckoned as though it had been seen in the petri dish. If the volume of the suspension was 30 cc., the lowest possible positive value for such a fossil is 150 per cc., the value computed when one is found in four micro-counts. Directly determined values for the larger fossils seldom approach this figure.

Many of the micro-count slides, and all the fossils removed from the petri dish, were made available for permanent reference by mounting in glycerine jelly. This medium has a rather unsatisfactory index of refraction, but has the great practical advantage of being miscible with water. Thus the entire lot of

fossils from 1 cc. of sediment can be directly transferred from water to the mounting medium, without risking the almost inevitable loss during passage through alcohols and clearing fluids.

Microfossil analyses are reported for 60 samples. Thirty-seven of these were taken from three borings in Linsley Pond, 9 were modern samples from the same lake, and the other 14 were taken from certain other lakes, as follows: Lake Quassapaug 5, Highland Lake 4, Lake Waramaug 3, East Twin Lake 1, Lake George (New York) 1. Of the ancient samples, all of those from borings L-9 and L-10 were laid down below the thermocline of the modern lake, and may be expected to reveal profundal conditions, an important consideration when chironomid larvae are to be used as indicators. Boring L-2, however, was taken in only 4 m. of water, and the upper part of the section is too "littoral" for satisfactory comparison. For this reason, and for others mentioned below, analysis of this boring was carried out only as far as the maximum of organic matter at the 11-foot level.

CHRONOLOGY.

The pollen-analytical chronology of the borings has been given in the first paper of this series (Deevey 1939), and may be recapitulated. The earliest periods (A-1, A-2) were characterized by a spruce-fir forest, the spruce reaching a maximum at the beginning of A-2. A pronounced maximum of pine occurred during period B-1, but evidence of this period is undeniable only in the two shallow-water borings L-1A and L-2. Three mixed-deciduous forest periods (C) have been recognized, oak-hemlock, oak-hickory, and oak-chestnut. The latter are well defined only in L-9 and L-10, as L-2 shows evidence of mixing and unconformities during the C periods, and deposition appears to have ceased at L-1A before period C-3. The general stratigraphy is summarized in Text Fig. 7; although the number of borings is too small to allow reliance on the reconstructed profiles, the irregularity of the present bottom below the site of L-2 suggests that some material has been removed from the top of this section and redeposited in deeper water. This suggestion is put forward on such slender evidence only because Miss Patrick, in the following paper of this series (1942) reports conspicuous abnormalities in the diatom flora of L-2.

ORGANIC MATTER

The curve for the ignitable organic matter in boring L-10 has been given by Hutchinson and Wollack; those for L-9 and L-2 are new, and all may be inspected in Text Figs. 1-3. It may be seen that there is a close similarity among all the curves.

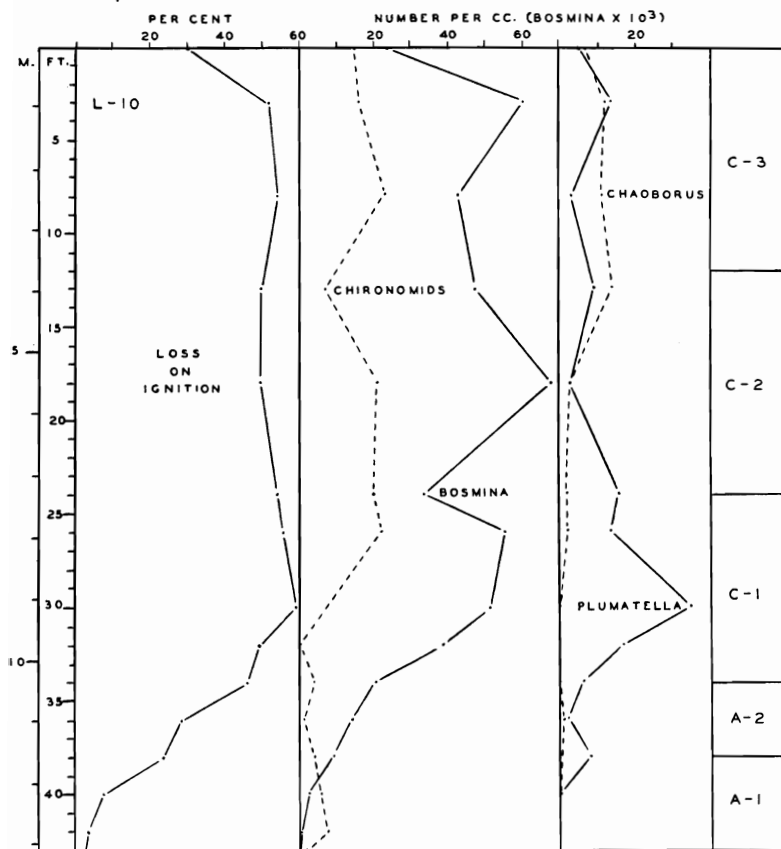


Fig. 1. Linsley Pond, boring L-10. Per cent loss on ignition and microfossils per cc. of wet sediment. Chronology at right.

The percentage of organic matter increased slowly, then rather more rapidly, reaching a maximum of 59 to 65 per cent early in C-1. Following this the values oscillated somewhat, but on the whole remained constant; a slight secondary maximum during C-3 is found in L-10 and L-9, but in L-2 the gradual decline was uninterrupted. All profiles show a marked fall between

the uppermost value for the consolidated sediment and the surface, the surface value plotted (30.2 per cent) being the mean of nine analyses of recent sediment taken at depths between 6.4 and 14.5 meters. This sharp decline was attributed by

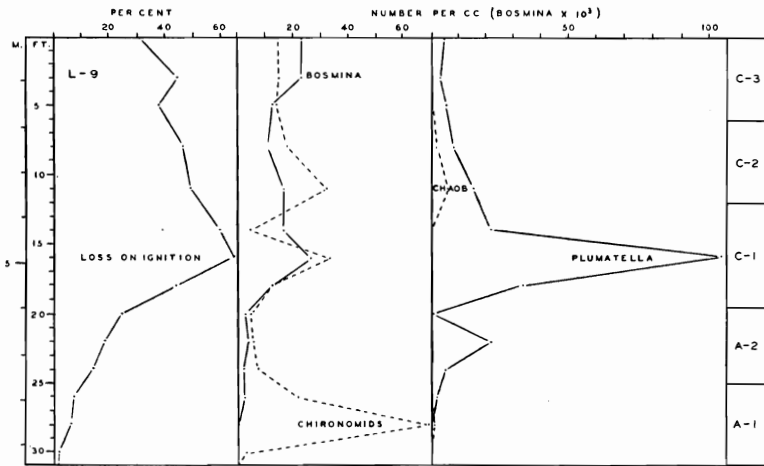


Fig. 2. Linsley Pond, boring L-9. Per cent loss on ignition and microfossils per cc. of wet sediment. Chronology at right.

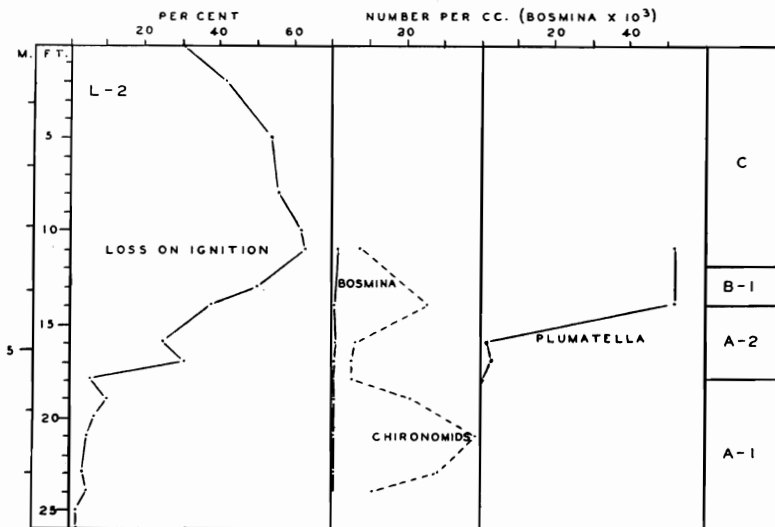


Fig. 3. Linsley Pond, boring L-2. Per cent loss on ignition and microfossils per cc. of wet sediment, so far as analyzed. Chronology at right.

Hutchinson and Wollack to increased erosion attendant on European colonization.

Among the several differences in detail, most of which are explicable on the ground that the total deposit differs considerably in thickness, one is particularly worthy of attention. The linear accumulation of silt during the A and B periods was distinctly greater at the sites of the shallow borings, L-2 and L-9, than at L-10. Part of this difference may be due to the fact that boring L-10 failed to penetrate to the underlying sand, but even if one or two feet of sediment be added to the bottom of this boring, some variation remains. Conversely, the gyttja is seen to have accumulated relatively more rapidly in the deeper parts of the basin. Such local variations, which are to be expected and which could easily be more striking in other lakes, serve to emphasize the value of a chronology in reconstructing the history of deposition.

As Hutchinson and Wollack have pointed out, the untreated curves for the percentage of organic matter may give a misleading impression of the course of development, because of such differences in rate of deposition as the ones just cited. As a first attempt to correct for this difficulty, they made two limiting assumptions; Assumption 1, that unit thickness of sediment was deposited in unit time, gives curves for organic matter (per unit volume of wet sediment) which are not essentially different from those of Text Figs. 1-3. Assumption 2, that unit mass of inorganic matter was deposited in unit time, however, has as its principal effect the stretching out of the curves below the maximum of organic matter, with a resulting emphasis on the exponential character of this part of the curves. It was recognized that both assumptions are unlikely, but if they are truly limiting, the real curve must lie between, and in examining the curves for microfossils presented below it is necessary continually to bear in mind that Assumption 2 is probably nearer the truth than Assumption 1.

BOSMINA.

QUANTITATIVE CHANGES.

The characteristic and easily identified cladoceran *Bosmina* is present in considerable numbers in nearly all samples analyzed, and reached the astonishing maximum of 67,400 per cc. at the 18-ft. level in L-10. Drawings of representative specimens are

given in Plate I, Figs. 8-11 and 14-16. The quantitative figures refer to half-specimens, as anterior and posterior halves occur in very nearly equal numbers; intact carapaces have been seen only in modern samples. Wasmund (1930) referred to the resistance of the chitin of *Bosmina* to decay. The results of the counts expressed in numbers per cc. of wet sediment are shown graphically in Text. Figs. 1-3. The curves for L-9 and L-10

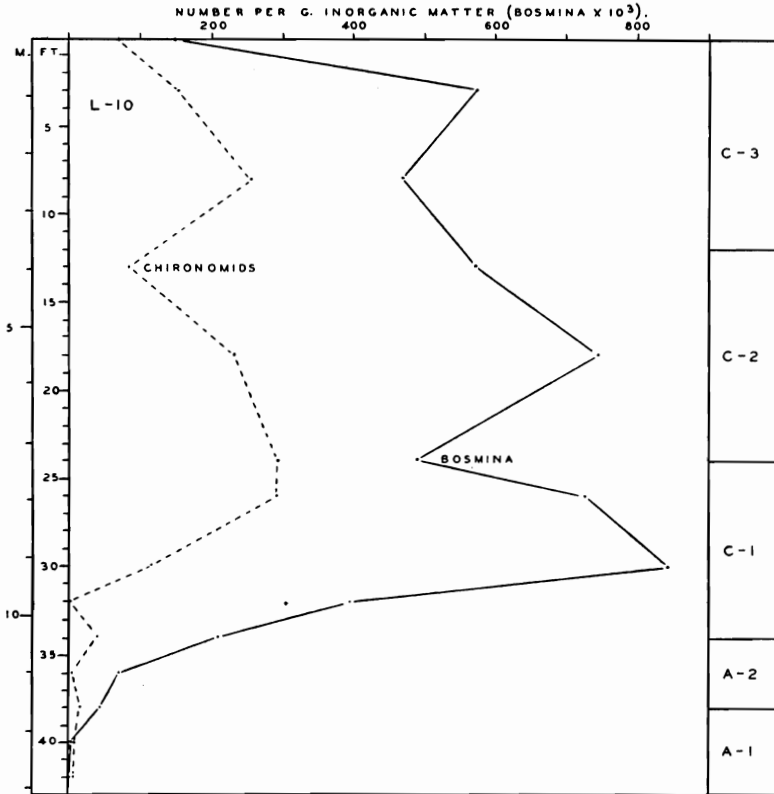


Fig. 4. Chironomid and *Bosmina* microfossils per gram of inorganic matter for boring L-10. Compare with Fig. 1.

in general resemble those for organic matter, particularly in the region of exponential increase during the A periods. After the attainment of the first maximum, which occurred at or near that of organic matter, some oscillation is found, but the variation throughout the period of "typological equilibrium" is little greater than that of organic matter.

It will be observed that although the curve of L-9 is on the whole correlative with that of L-10, the maximum numbers are considerably smaller at the former boring, and at L-2 the numbers are negligible, although again a slight rise is found at the level of maximum organic matter. It might at first be supposed that these differences are due to the greater thickness of water over the deeper borings; there is, however, no evidence from the recent counts that deeper stations receive more *Bosmina*. The counts on the nine modern samples range from 14,200 to 42,100 per cc., with no tendency to vary consistently with depth. It is not improbable that the profile-bound density currents demonstrated by indirect means by Hutchinson (1941) may be the agency responsible for concentrating the *Bosmina* in the deeper waters during most of the deposition.

Although it is conceivable that the abnormally high phytoplankton:zooplankton ratio of Linsley Pond may be associated with the cultural modification of the drainage basin, the variation of *Bosmina* with depth between L-9 and L-10 makes it impossible to consider this matter further at present.

In Text Figs. 4 and 5 the values of *Bosmina* per gram of inorganic matter are shown; this treatment of the data amounts to the acceptance of Assumption 2, but without distorting the time scale. The method of presentation is justified, moreover, by the fact that the samples may have dried unevenly, so that a comparison on the basis of unit weight is desirable. The resemblance of the curves to the corresponding ones of Hutchinson and Wollack is impressive.

QUALITATIVE CHANGES.

The quantitative changes shown by *Bosmina* in the sediments can be divided into two phases, the initial rapid increase and the period of approximate stability. It is very interesting, therefore, to find that a corresponding qualitative change took place. It is difficult, if not impossible, to make precise determinations on the basis of the half-carapace, since the contour of the back cannot be satisfactorily reconstructed. The posterior portions of carapaces from the older sediments are, however, in general distinguishable from those in the upper parts of the profile by their more elongate, and in young specimens, often ventrally denticulate, mucrones. A fortunate occurrence of a postabdomen associated with a posterior carapace fragment has led Mr. T. S. Austin (Appendix I) to identify the older form as

B. coregoni longispina Leydig, while the more recent form with a short mucro is still abundant in the lake and is undoubtedly referable to *B. longirostris* (O. F. M.). The change in mucro length takes place within a very narrow vertical range, beginning just before the maximum of organic matter (32 feet in L-10, 18 feet in L-9), and being consummated at the level of maximum organic matter in each profile. This change therefore would appear to represent the replacement of *B. coregoni longispina* by *B. longirostris* at the end of the period of increasing organic sedimentation. A few specimens with long mucrones

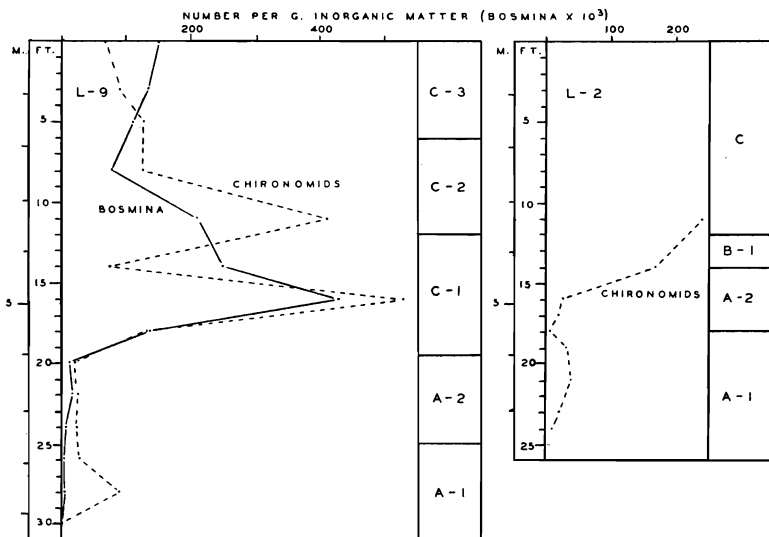


Fig. 5. Chironomid and Bosmina microfossils per gram of inorganic matter for boring L-9 (left) and boring L-2 (right). Compare with Figs. 2 and 3.

may be still found in both the upper sediments and in the modern plankton of the lake; inspection of material from the latter source, however, shows these to be forms of *longirostris* and not *coregoni longispina*.

Mr. Austin, who has examined all available plankton samples from Connecticut, reports in Appendix I that *B. coregoni longispina* is mainly found in the less alkaline (<38.6 mgr. per liter HCO₃), plankton poor (chlorophyll ≤ 4.8 λ per liter) lakes of the highlands, *longirostris* in the more alkaline (> 20.6 mgr. per liter HCO₃) plankton rich (chlorophyll > 4.8 λ per

liter) lakes largely in the central lowland. The correlation with alkalinity is less good than that with phytoplankton; such an association is not in accord with observations made by Mr. Austin on material from other parts of North America, but is apparently supported by the general experience of European workers (Rylov 1935).

ALLOMETRIC GROWTH OF A BIOCOENOSIS.

Hutchinson and Wollack have made it clear that the increase of organic matter in the sediments follows a curve roughly resembling the sigmoid or logistic curve for the growth of organisms and homogeneous populations, and that the exponential rise during the early stages of development is independent of the method of treatment of the data. It has been seen that *Bosmina* increased in a strikingly similar way, but the rate of increase was greater for *Bosmina*. In the language of the analogy between the organism and the biocoenosis, this evidently means that a sort of allometric growth occurs, the rate of growth of the part differing from that of the whole, as the claw of the fiddler crab grows faster than the animal as a whole (Huxley 1932), or as the water content of an embryo increases less rapidly than the total weight (Needham 1934). If the total organic matter of the sediments is a reasonable estimate of the organic matter produced by phytoplankton and littoral vegetation, and if the *Bosmina* content of the samples is also a reasonable estimate of the quantity of zooplankton produced, the relative growth of part and whole can legitimately be examined.

In Text Fig. 6 the logarithm of total organic matter per cc. of sediment is plotted against the logarithm of *Bosmina* half-specimens per cc. for borings L-10 and L-9. The points used are those for the period of exponential increase only, i. e. from the first appearance of *Bosmina* through the period of maximum organic matter. Beyond this level, although there is no break in the slope of the lines, the points move up and down in irregular fashion. The lines drawn through the points have been fitted by the method of least squares, and the equations derived are

$$\begin{array}{lll} \text{for L-10, } y = bx^k, & k = 5.10, & b = 2.68 \cdot 10^{-5} \\ \text{for L-9, } y = bx^k, & k = 4.14, & b = 1.17 \cdot 10^{-4} \end{array}$$

where $y = \text{Bosmina}$, $x = \text{total organic matter}$, $b = \text{a constant}$

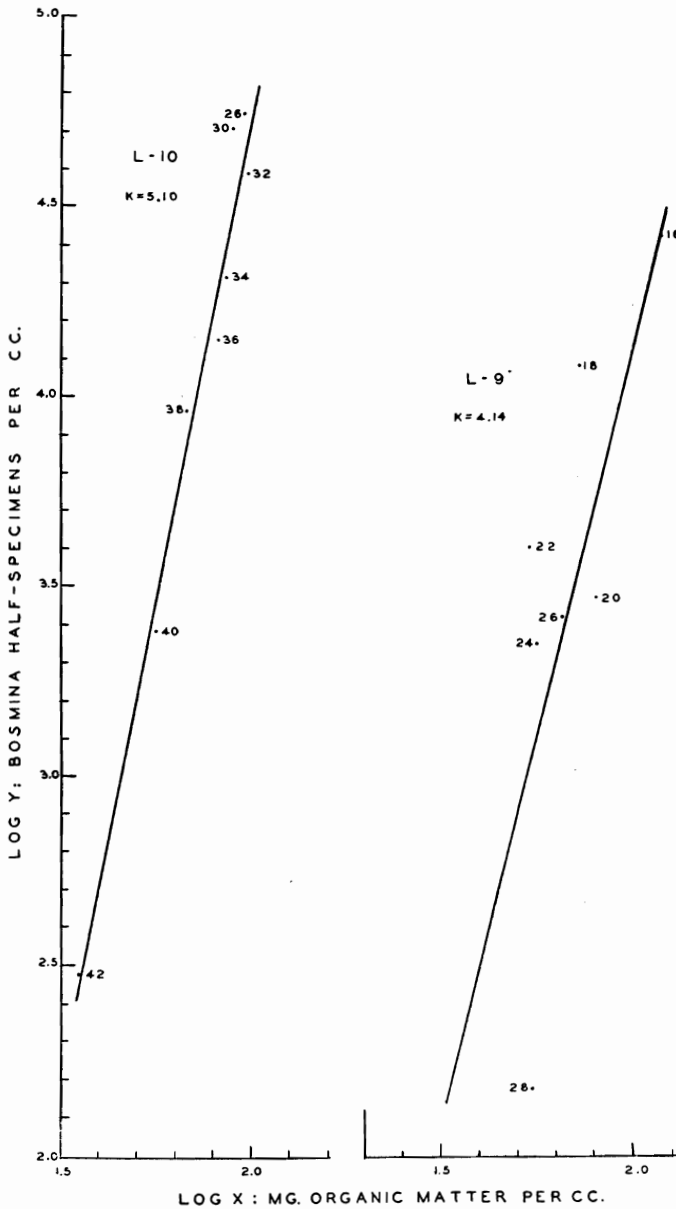


Fig. 6. Double logarithmic plot of *Bosmina* microfossils per cc. of wet sediment against mg. of organic matter per cc. for borings L-10 and L-9. The lines are graphs of the equation of allometric growth, $y = bx^k$ (see text).

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giving the value of y when $x=1$, and k =the "allometry constant," or the slope of the line when a double log plot is made.

The values for L-10 fall very close to the line calculated from the equation, those for L-9 give a somewhat less perfect fit, while at L-2 the number of *Bosmina* is too small, and the increase of organic matter too irregular, to bring out the relation. The equation derived is identical in form with that for the allometric growth of organisms, whether morphological or chemical entities are considered, and this identity provides the strongest possible support for the analogy between the growth of organisms and of biocoenoses.

A constant relation between the part and the whole during development is probably to be expected when major constituents of the whole, such as zooplankton, phytoplankton, rooted vegetation, etc., are considered. It is rather surprising, however, to find the relationship so clearly shown over such a long period of time by a single genus. One might expect species substitution to play a part, perhaps in changing the value of the constant of allometry. That the lines of Text Fig. 6 remain straight in spite of a conspicuous example of species substitution presumably means that *Bosmina* is an exceptionally satisfactory indicator of total zooplankton.

COMPUTATION OF POST-GLACIAL TIME.

Given the number of fossil *Bosmina* carapaces incorporated in a unit volume of sediment, we shall be in a position to estimate the length of time occupied by deposition if we can learn the mean number of *Bosmina* in the modern lake and their rate of loss to the bottom. Such an estimate of post-glacial time would be analogous to the one obtained by Lohmann (1909) for the rate of increment of marine deposits on the basis of the standing crop of *Coccolithophoridae*. The method, at least in theory, is capable of considerable refinement, and yields an estimate that is wholly independent of such geologic approaches as the degree of weathering of till sheets, the recession of Niagara Falls, and the varved clay chronology.

Unfortunately our limnological information is not yet sufficiently exact to permit the confident application of this procedure. Difficulties arise both in respect to the standing crop of *Bosmina* in Linsley Pond and to the annual production.

The mean number of *Bosmina* per liter, according to Doctor Riley's zooplankton counts (weighted for the lack of midsum-

mer data) is about 15. This value, however, is certainly too low, as the individual counts are based on the concentration of 200 cc. of catch taken in the Nansen water sampler. Only three series of samples taken in January, July, and August with the Juday 10-liter plankton trap, which is much more reliable, are at hand, and these Mr. Austin loaned to the author; the mean number of *Bosmina*, weighted for the volume of the lake at each level sampled, is 29.6 per liter. This very inadequate average must be used in default of more extensive data, which will soon be available.

The mean longevity and mean number of instars of *Bosmina* in the lake cannot be ascertained at present; when we fall back on laboratory experiments we find that although the requisite information is available for several species of cladocerans, *Bosmina* is not among them. Wood, Ingle, and Banta (1939) found that under optimum culture conditions at 25° C. the mean length of life of *Daphnia longispina* was 29.6 days, and the mean instar number 18.1, from which the three pre-adult moults should be subtracted. MacArthur and Baillie (1929) give data for the longevity of *Daphnia magna* at different constant temperatures. Inspection of the few pertinent observations of several other authors (especially Papanicolau 1910, Rammner 1929) indicates that other species studied do not differ widely from the above. But in view of the almost total lack of relevant facts, it will be understood that the following computation of post-glacial time is largely guesswork, and is intended merely as a sketch of the method.

Mean standing crop of <i>Bosmina</i>	29.6 per l.
Number of generations per year:	
1 per month, Apr. 15–Oct. 15	6
1 every 90 days, Oct. 15–Apr. 15	2
	—
Total	8
Number of instars	15
Annual production of carapaces	3550 per l.
	=2380 per cm. ²
	—
Mean number of <i>Bosmina</i> , recent samples	11,500 per cc.
(1) On this basis, 1 cc. takes to accumulate	4.83 years
Mean number of <i>Bosmina</i> , organic matter maximum to 3-ft. level, L-9 and L-10	17,100 per cc.
(2) On this basis, 1 cc. takes to accumulate	7.19 years
Mean number of <i>Bosmina</i> , organic matter maximum to 3-ft. level, L-10 only	25,500 per cc.

(3) On this basis, 1 cc. takes to accumulate 10.7 years

Mean accumulation of sediment from organic
matter maximum to surface, L-9 and L-10 7 m.

(1') On basis of estimate (1), 7 m. took to accumulate 3380 years

(2') On basis of estimate (2), 7 m. took to accumulate 5020 years

(3') On basis of estimate (3), 9.15 m. of L-10 took to
accumulate 9790 years

On Assumption 2 of Hutchinson and Wollack, time
elapsed since organic matter maximum is 30% of
total time of deposition

Estimate (1') becomes 11,300 years

Estimate (2') becomes 16,750 years

Estimate (3') becomes 32,600 years

Some insight into the validity of these figures may be had by comparing estimates (1), (2), and (3) with direct measurements of the annual accumulation of lake sediments in containers. Reissinger (1932) reports that the average annual ac-

EXPLANATION OF PLATE I.

Selected microfossils from the sediments of Linsley Pond.

All figures drawn with the aid of the camera-lucida.

Fig. 8. Posterior part of carapace of *Bosmina coregoni longispina* from L-10, 38 ft. \times 70.

Fig. 9. Another specimen from L-10, 38 ft. \times 70.

Fig. 10. Another specimen from L-10, 36 ft. \times 70.

Fig. 11. Anterior part of another specimen from L-10, 36 ft. \times 70.

Fig. 12. Postabdomen of *Alona affinis* from L-9, 24 ft. \times 100.

Fig. 13. Broken postabdomen of *Eurycercus lamellatus* from L-2, 14 ft. \times 30.

Fig. 14. Postabdomen of *Leydigia quadrangularis* from L-9, 24 ft. \times 100.

Fig. 15. Anterior part of carapace of *Bosmina longi rostris* from L-10, 32 ft. \times 70.

Fig. 16. Another specimen from L-10, 30 ft., lateral view. \times 70.

Fig. 17. Posterior part of another specimen from L-10, 30 ft. \times 70.

Fig. 18. Valve of carapace and postabdomen of *Alona quadrangularis* from L-10, 18 ft. \times 70.

Fig. 19. Valves of carapace of *Chydorus faviformis* from L-10, 30 ft. \times 70.

Fig. 20. Head of Tanytarsus from L-9, 28 ft., ventral view. \times 70.

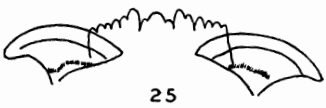
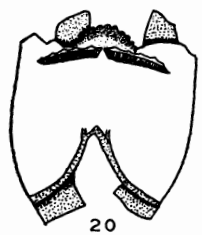
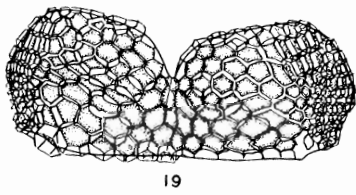
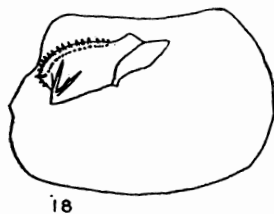
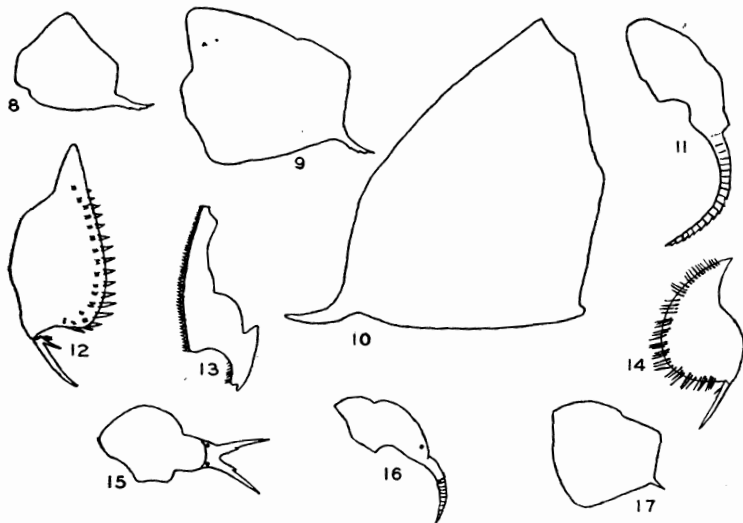
Fig. 21. Mandible and fan of Chaoborus from L-10, 8 ft. \times 70.

Fig. 22. Labium and paralaial plates of Chironomus, *sensu lato*, probably Glyptotendipes, from L-10, 8 ft. \times 70.

Fig. 23. Supposed cyst of a suctorian, perhaps Podophrya, from L-10, 26 ft. \times 70.

Fig. 24. Labium and paralaial plates of Chironomus, *sensu lato*, probably Endochironomus, from L-2, 21 ft. \times 70.

Fig. 25. Labium and paralaial plates of Chironomus, *sensu stricto*, from L-10, 30 ft. \times 70.



cumulation over periods as long as 12 years is as follows: Alpesee, 4.1 kg. dry weight per square meter, Niedersonthofener See 6.1 kg., Starnberger See 0.51 kg. Scott and Miner (1936) obtained a value of 2.32 kg. per square meter in Winona Lake and 1.4 kg. in Tippecanoe Lake, Indiana. If estimate (1) is adopted, and the average dry weight of modern samples from Linsley Pond, 0.2708 g. per cc., is used, the sediment accumulates at a rate of 0.56 kg. per sq. m. per year; other estimates yield still lower values. Thus it appears that the Linsley calculations assume a rate which is somewhat too low, but when it is realized that the first two of Reissinger's lakes receive much fluvial material, and that the Indiana lakes are depositing an impure marl, one may suspect that the error is not great.

Of the three estimates of post-glacial time, estimate (1') appears to be the most probable. Estimate (2') is too high if, as seems likely, more *Bosmina* were produced during most of the period of typological equilibrium than at present. Estimate (3') is clearly too high, as *Bosmina* fossils seem to have been concentrated in the region of boring L-10 by density currents; the estimate has been included in order to emphasize the need for several borings when such calculations are to be made. All the estimates are too high if the shrinkage of the samples through drying has been appreciable. It may be observed, on the other hand, that if some of the annual production of *Bosmina* is lost through predation, all the estimates are too low in proportion to the loss. Pelagic plankton-feeding fish do not occur in Linsley, and until further evidence is at hand the author leaves open the questions, first, whether the consumption of *Bosmina* by *Chaoborus* is significant, and second, if so, whether a *Bosmina* carapace might not remain recognizable after predatory attack by *Chaoborus*.

Taking the estimate of 11,300 years at its face value, the agreement with the results of other methods is sufficiently close to be encouraging. But further discussion would be premature, as it has already been pointed out (Deevey 1939) that there is no reason to expect strict contemporaneity of origin for the earliest lake deposits in a region occupied by a stagnant ice sheet.

OTHER CLADOCERA.

Although the carapaces of cladocera other than *Bosmina* are frequently found in the sediments of Linsley Pond, specific

identifications are usually possible only in the fortunate circumstance that a postabdomen is retained between the valves. (Plate 1, Fig. 18). The remarkable form *Chydorus faviformis* Birge (Plate 1, Fig. 19), however, may readily be recognized by its carpace alone, and *Eurycercus lamellatus* (O.F.M.) (Plate 1, Fig. 13) has been identified by its highly distinctive postabdomen. The list of recognizable species is as follows:

Chydorus faviformis Birge: Period C-1 to recent; borings L-9 and L-10; most abundant per cc. during C-2.

Eurycercus lamellatus (O. F. M.): Period A-2 to C-2; all borings; recent only in Highland Lake.

Alona quadranglaris (O. F. M.) (Plate 1, Fig. 18): Period C-1 to C-2; borings L-9 and L-10.

Alona affinis (Leydig) (Plate 1, Fig. 12): Period A-2 and C-2; boring L-9.

Leydigia quadrangularis (Leydig) (Plate 1, Fig. 14): Period A-2 and C-2; borings L-9 and L-10; recent in Linsley.

In addition to the above fossils, the even more bizarre species of *Chydorus*, *C. bicornutus* Doolittle, has been seen in recent samples from Highland Lake and Lake Quassapaug, and is almost certain to be found in more ancient sediments.

These species appear to have no typological or climatic significance, as most of them are common, widely distributed animals of the weedy littoral, while the *Chydorus* is a rare form whose distribution is poorly known. Only *Chydorus faviformis* occurs in sufficient numbers to permit a reasonable estimate of the relative frequency; if this species should eventually prove to be a warm stenotherm, it will be interesting to recall its relative abundance during C-2, the time of the supposed climatic optimum.

Cladocera have frequently been seen as microfossils by botanists and geologists, but specific identifications have seldom been made. Tidelski (1929), however, records *Eurycercus lamellatus*, *Alona quadrangularis*, and *Sida crystallina* (O. F. M.) from lake sediments of boreal and pre-boreal date in northern Germany, and Messiatzev (1924) recognized fifteen species in deposits of three Russian lakes in the vicinity of Moscow.

CHIRONOMIDS.

QUANTITATIVE CHANGES.

The curve showing the abundance of recognizable chironomid fragments in boring L-10 is reproduced in Text Fig. 1. It is

not absolutely certain that the number of heads found is proportional to the number of living larvae, since some fossils may represent the cast skins of earlier moults. If this complicating factor is ignored as systematic and therefore relatively unimportant, the strong qualitative resemblance between this curve and those for organic matter and *Bosmina* may be taken to indicate that the total bottom fauna increased rapidly to a maximum at the time of maximum organic matter, and remained approximately stable thereafter.

The corresponding curves for L-9 and L-2, however, show a slightly different state of affairs, for in place of a gradual increase during the A periods a pronounced maximum is found during A-1. This maximum is composed almost exclusively of *Tanytarsus*. If Assumption 2 is correct, or nearly so, the number of larvae produced in unit time during the early periods was much smaller than these graphs suggest, as may be seen from Text Figs. 4-6. Indeed the improbability that the number of benthic animals declined during the steady rise of organic matter and zooplankton constitutes one of the best arguments for the approximate validity of Assumption 2. In any case a maximum of *Tanytarsus* does not imply excessive benthic production, as these larvae are small, weighing about one-thirtieth as much as a large *Chironomus*. It is somewhat surprising to find that the bottom fauna during the *Tanytarsus* period was more abundant on shallower bottoms (L-2 and L-9) than on deeper; this form of chironomid distribution characterizes the modern Lake Quassapaug (Deevey 1941b) as well as most *Chironomus* lakes, and is generally attributed to a lower oxygen content and more strongly reducing conditions in the lower part of the hypolimnion. The "classical" *Tanytarsus* lakes, however, usually show a much more uniform vertical distribution (Lundbeck 1936, Deevey 1941b).

QUALITATIVE CHANGES.

As the taxonomy of chironomid larvae is in an unsatisfactory condition at best, and as many important taxonomic characters, such as the antennae, various bristles, and the entire larval body are missing from the fossils, specific identifications are not practicable. Much can be learned nevertheless from the generic identifications, which can usually be made with ease. The occurrence of the principal genera in all the borings and

modern samples is tabulated in Table 1. A synopsis of the characters used is as follows:

In general the author follows Johannsen (1937a, 1937b) in the use of generic names in the broad sense. *Tanytarsus* can be recognized almost instantly by the high sockle of the antenna (Plate 1, Fig. 20); failing this, the short, very wide paralabial plates, almost meeting in the mid-line, are also useful. Occasionally it is possible to identify the subgenus *Stempellina* by the palmate process on the antennal sockle. *Pseudochironomus*, characterized by nine teeth on the labium, has been seen only rarely. *Chironomus* (*sens. lat.*), with broad, striated paralabial plates, may belong to several subgenera; most of those with an even number of labial teeth are close to if not congeneric with *Endochironomus* (Plate 1, Fig. 24) and have been so designated; those with an odd number of teeth also have relatively narrow paralabial plates with crenulate cephalic margins and closely resemble *Glyptotendipes* (and *Limnochironomus*) (Plate 1, Fig. 22). *Chironomus* (*sens. str.*) has a trifid middle labial tooth and broad paralabials; the fossils are indistinguishable from *C. decorus* and *C. hyperboreus* of the modern Linsley. "Tanypus" includes the Tanypodinae, which are easily referable to the proper subfamily on the basis of the characteristic labium and the retractile antennae; the first joint of the antenna can usually be seen within the head. "Orthocladius" refers to the subfamily Orthocladiinae, in which the paralabials are absent or reduced; some of these fossils are probably congeneric with *Trissocladius*, a type common in Connecticut highland lakes, but others are not, and resemble the genera *Brillia* and *Metriocnemus*. Precise determination of the Orthocladiinae, however, is not feasible in the absence of several important parts of the head. A specimen belonging to the Diamesinae was once recognized through the fortunate preservation of the antenna, but if others are present they have undoubtedly been confused with the Orthocladiinae.

The very great diversity of the chironomid fauna revealed in Table 1 limits severely the number of positive statements that can be made. Several important conclusions can, however, be drawn:

1. The association of *Tanytarsus* with the earliest period (A-1) is sufficiently strong to allow the lake at this time to be described as a *Tanytarsus* lake. Larvae of this genus nevertheless persisted throughout the development of the biocoenosis,

L-2	11 ft.	.0776	62.3	1	0	2	1	1	0	1	1	1	6	1.20	0	51.5
	14	.2481	37.7	10	2	1	1	1	0	4	5	23	0.75	0	51.5	
	16	.3520	24.8	1	0	1	1	0	2	0	1	6	0.88	0	1.5	
	17	.4142	30.1	0	3	0	0	1	1	0	1	5	0.45	0	2.5	
	18	.9098	5.5	1	0	0	0	2	0	0	2	5	0.30	0	0	
	19	.7712	9.9	12	1	1	5	1	1	0	1	21	0.45	0	0	
	21	1.1383	4.8	24	2	6	0	0	0	0	6	38	0.15	0	0	
	23	1.4795	8.7	24	5	3	0	0	0	1	3	28*	0.075	0	0	
	24	1.5790	4.7	5	3	0	0	0	0	0	3	11	0.10	0	0	
LIN	6.4 m.	.3396	31.2	5	1	1	0	2	2	5	5	19	21.6	3	5.5	
	8	.7514	27.0	3	4	3	2	2	2	1	16	51	35.6	6	16.5	
	9	.1990	31.9	2	0	0	3	4	4	2	4	15	23.8	2	5.0	
	10	.1350	31.2	1	0	0	0	1	1	1	2	5	18.4	3	1.5	
	11	.1346	27.6	1	0	0	0	1	1	1	0	3	14.6	3	2.0	
	13	.2532	31.0	3	1	1	2	2	1	1	5	15	42.1	14	3.0	
	13	.1436	37.0	1	1	1	0	1	0	0	0	3	21.6	3	2.5	
	14.5	.1878	27.4	0	2	1	1	1	1	3	3	11	14.8	10	2.5	
	14.5	.2926	27.2	1	2	0	0	0	0	3	3	7.3*	14.2	11.8	1.4	
QS	5 m.	.4735	8.7	2	3	0	3	0	0	3	3	14	0.6	0	0.5	
	9.5	.2624	21.8	23	2	1	3	5	5	10	5	49	5.6	2	1.0	
	10	.2362	19.4	9	3	0	1	1	1	13	5	29*	3.7	1	0	
	12	.1462	24.0	25	3	0	1	8	7	7	2	38*	5.0	5	0	
	15	.1030	24.5	13	0	0	1	4	3	3	4	25	5.5	5	1	
HI	5.9 m.	.1588	25.6	5	5	0	4	0	0	10	3	27	0.15	2	0.5	
	9	.1140	19.0	18	3	0	0	0	0	4	1	26	0.45	0	0	
	11	.0924	25.6	5	1	3	0	0	0	8	1	18	1.05	5	0	
	14.8	.0785	26.4	0	2	6	0	0	0	2	0	10	0.75	2	0	
WAR	7.6 m.	.3531	12.3	12	6	1	2	1	6	10	38	0.6	0.6	5	2.0	
	9	.2333	16.1	5	1	1	2	1	1	5	16	0.6	0.6	1	0.5	
	11.2	.1638	21.4	2	0	0	0	5	1	3	11	0.45	0.45	5	0.5	
ET	19.1 m.	.1081	28.2	0	0	2	1	0	5	2	2	6.3*	0.5	0	0.5	
GEO	43 m.	.1830	18.4	0	1	1	0	0	0	0	0	2	5.0	0	2.0	

* These figures do not represent the total number of chironomids included in the other columns, as the quantity of sediment examined was not exactly 1.00 cc.

and are still present in the lake, although in very small numbers in the deep water. It cannot be doubted that the early lake was qualitatively as well as quantitatively oligotrophic.

2. The earliest members of the genus *Chironomus* to appear (during A-1) are representatives of the mesotrophic subgenera, probably *Endochironomus* and *Glyptotendipes*. These larvae were associated with *Tanytarsus* in the formation of a mixed fauna, as they are in modern mesotrophic lakes, e.g. Highland Lake, Connecticut, and several Japanese lakes.

3. *Chironomus* (*sens. str.*) was the latest important indicator to appear, but it occurs in borings L-2 and L-9 at unexpectedly early levels (late A-1 and A-2). Although of course proof is lacking, this latter circumstance probably reflects the peculiar difficulty described in an earlier paper (Deevey 1941b), namely that "mesotrophic *Chironomus*," indistinguishable as adults from eutrophic species of the genus *sensu stricto*, lack ventral blood gills as larvae and occur in association with an oligotrophic oxygen curve.

4. The distribution of "*Orthocladius*" in borings L-9 and L-10 shows a curious lacuna, in that an early and a late group of occurrences is separated by a prolonged period (late A-1 to early C-1) during which the larvae of this subfamily were apparently absent. Further work combined with more fortunate preservation may eventually show that the early group belongs to a truly oligotrophic genus, e.g. *Metriocnemus*, while the late specimens are *Trissocladius*.

5. In expected correspondence with its known modern distribution in lakes of various types, "*Tanytarsus*" occurred with great indifference throughout the development of Linsley.

6. Despite the great diversity of recent "fossils," the modern samples in general reflect the type of chironomid fauna expected from limnological studies. The modern Linsley samples show *Chironomus* (*sens. str.*) to be the most abundant (and of course if weights could be determined, these larvae would greatly outweigh the rest). Highland Lake shows an admixture of *Tanytarsus* and *Endochironomus*, with *Chironomus* (*sens. str.*) lacking. Lake Waramaug samples contain *Chironomus* (*sens. str.*) mixed with *Tanytarsus* at shallower stations, as do the modern Ekman samples. *Tanytarsus* predominates in the samples from Lake Quassapaug, a modern *Tanytarsus* lake, although the strong admixture of *Chironomus* (*sens. str.*) is surprising. A single sample from Lake George

contained one "Orthocladius" (typical of the lake) and one Chironomus (*sens. lat.*). The single sample from East Twin Lake is less representative, since the typical "mesotrophic Chironomus" did not occur, but was replaced by Chironomus (*sens. lat.*).

CHAOBORUS.

The recognizable fragments of Chaoborus are various, and include the mandible with premandibular fan attached (Plate I, Fig. 21), the entire ventral portion of the head showing the bases of the antennae and all mouth parts with the unfortunate exception of the prelabral leaf-like appendages (see Johannsen 1934, Fig. 148), and the pupal breathing tube (Johannsen, Fig. 172). This diversity implies that the numbers of fragments are probably not proportional to the numbers of living larvae. The numbers are astonishingly small in view of the enormous abundance of these larvae in the modern lake, and this paucity must mean that Chaoborus exuviae tend to float to the surface of the lake and are then blown elsewhere. So far as can be judged in the absence of the pre-labral appendages and the anal fan, the fragments refer to *C. punctipennis*, (Say), which is the species of the modern lake.

The records for boring L-10 (Text Fig. 1) include one occurrence during A-2, as do those for L-2, but all other fragments seen occurred much later, with the maximum falling in C-2. The only records for boring L-9 also refer to the latter period. If the numbers per cc. or per unit dry weight correspond even approximately to the actual numbers of larvae, the bathyphilous vertical distribution shown by the modern Chaoborus has persisted since C-2. In spite of the numerous uncertainties, it is difficult to escape the conclusion that the oxygen content of the hypolimnion fell to very low values at least as early as that time. In partial explanation of the early occurrences it may be pointed out that Chaoborus is occasionally taken in Lake Quassapaug, as well as in more oligotrophic lakes; in Finland it sometimes is associated with *Mysis relicta* (Valle 1936).

PLUMATELLA.

The statoblasts of Plumatella are readily recognized, and they are found in large numbers in all the borings, as well as in small numbers in the modern samples. Dr. Mary Rogick, who has examined the specimens, reports in a private communication that, so far as can be judged without the colonies, they belong

to *P. repens*. This is a highly polymorphic and widely distributed species, and no typological or climatic significance can be attached to the occurrence of the animals as such. Their greatest value appears to consist in the fact that they are in general epiphytic, and thus can supply indirect evidence of the relative abundance of littoral vegetation.

In Text Figs. 1-3 it may be seen that the maximum abundance per cc. is precisely correlated with the maximum of organic matter; the peaks are even more sharply emphasized when the data are converted to unit dry weight. Such a phenomenon, occurring as it does in all the borings, can scarcely be meaningless. In the following paper of this series Miss Patrick reports that epiphytic diatoms were especially abundant at this time, particularly at boring L-10. As there is no evidence of drying in the shallower borings, such as would be expected if the lake level was ever appreciably lower (see Pt. II), it appears highly probable that littoral vegetation, with its epiphytic diatoms and *Plumatella*, grew at greater depths and approached the sites of borings L-9 and L-10 more nearly than at present. As the epiphytic forms (both diatoms and *Plumatella*) declined in abundance in the subsequent deposits, and as one must suppose that they did not originate at their present sites, but were floated there, it follows that in addition to the vertical restriction of the vegetation zone which has clearly taken place, an actual decrease in the available substratum has occurred. If this reasoning be accepted, it can plausibly be argued that the *Plumatella*—organic matter maximum represents the last stage of the increase of productivity in which the productivity was proportional to the standing crop of phytoplankton, and the subsequent increase in phytoplankton, if any, merely reduced its own supply of light, bringing about the lack of correlation between productivity and standing crop shown for the modern lake by Riley. In other words, early in C-1 the most favorable balance of transparency, standing crop of phytoplankton, and littoral vegetation was attained, and any further increase in phytoplankton (at the surface) was compensated by a decrease in the quantity of higher plants.

OTHER POLYZOA.

Statoblasts of *Pectinatella magnifica* Leidy and *Cristatella mucedo* Cuvier are known to occur in the sediments of the modern Linsley; a few counts made during the study of Ekman

samples for bottom fauna indicate that their density is about 0.01 per cc., so it is not surprising that these objects occur only rarely in the microfossil analyses of 1 cc. The records include five statoblasts of *Pectinatella*, one during A-1 in L-2 (in a pollen preparation from 21 ft.), one during C-3 in L-10, and three in recent samples from Lake Quassapaug. *Cristatella* has appeared only once, during A-2 in L-9.

Cristatella is of no value as an ecological indicator, as it is very widespread and indiscriminate in its choice of habitat. The very early occurrence of *Pectinatella* is of interest, however, as this species is a warm stenotherm (Brown 1933), requiring a temperature of 18° to 20° C. for its development. Evidently, despite the cool-temperate climate indicated by the spruce-fir forest of period A-1, the surface temperature of the lake reached these values in summer.

FONTINALIS.

Considerable numbers of fragments of the aquatic moss *Fontinalis* were found in the sediments of period A-1 in borings L-2 and L-9. In boring L-9 they occurred at only one level (28 ft.) while in L-2 their distribution spans the latter half of the period. If these fragments were not derived from plants living nearby, but were carried from some point further up the slope, it seems likely that some would have been recorded from L-10. While *Fontinalis* is now known from the modern lake only in very shallow water, so that the evidence indicates a greatly increased transparency during A-1, the extent of this increase cannot be certainly fixed. In Wononscopomuc Lake, one of the most transparent of Connecticut lakes, the Secchi disc disappears at about 9 m., while the lower limit of "rooted" vegetation (charophytes) lies at about 12 m. In Walden Pond, Massachusetts (Deevey 1942), *Fontinalis* grows as deep as 16 m., but the transparency determination (6 m.) is certainly too low. In Crater Lake, Oregon, (Hasler 1938) the maximum transparency is 40 m., while *Fontinalis* has been taken at 120 m. It appears that if the deepest occurrence of this moss in the ancient Linsley (14.5 m.) can be attributed to plants growing *in situ*, the most reasonable estimate of the transparency is 10-12 m.

OTHER MICROFOSSILS.

The list of microfossils discussed in the foregoing sections is not unimpressive, including as it does six species and one sub-

species of cladocera, representatives of at least six genera and four subfamilies of Chironomidae, Chaoborus, three species of Polyzoa, and one species of aquatic moss; many of these are here recorded as fossils for the first time. It is certain, however, that the list can be materially augmented with the assistance of specialists in certain groups, the outstanding omissions being among the mites and ostracods.

Other objects seen include the following: Ceratopogonidae, not identified, included with Chironomidae; Sialis jaws; cysts of some suctorian, perhaps Podophrya (Plate I, Fig. 23); supposed rotifer and gastrotrich eggs; oogonia of charophytes. Intact specimens of cyclopoid and harpacticoid copepods have frequently been seen in recent samples, but appear not to be preserved in the older sediments. Nothing can be said about any of these fossils beyond the fact of their occurrence, as specific identifications have not been made, and as their occurrence is too infrequent to justify a discussion of their temporal distribution. Sponge spicules occurred frequently in Miss Patrick's diatom preparations, and Dr. Minna Jewell reports on these in Appendix 2.

The collection is remarkable for certain omissions. Many presumably resistant remains have never been found, despite careful search for at least some of them. Among those that might have been expected, the following suggest themselves: fragments of copepods, cyst capsules of Canthocamptus, oligochaet cocoons, loricae of rotifers, tests of rhizopods, seeds of aquatic plants. Some of these are certain to be found as work progresses and as larger samples are analyzed; others, such as copepod and oligochaet remains, may not be sufficiently inert chemically to permit fossilization.

It would be gratifying to be able to state the belief that no important microfossil has been overlooked in the analysis of the Linsley borings. Experience has shown, however, that this is very unlikely. Although unfamiliar objects have been scrutinized with great care, it is certain that one tends not to see even the most distinctive fossils unless he is prepared to see them. For this reason, and because the competence of the individual investigator is bound to be limited by his previous zoological or botanical training, it is highly desirable that specialists of many sorts collaborate in the prosecution of biostratonomy.

To be continued.