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# The postglacial development of the Chironomidae and Chaoborus faunae (Diptera) of the Schohsee

by Wolfgang Hofmann

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# The postglacial development of the Chironomidae and Chaoborus faunae (Diptera) of the Schöhsee

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(With Plate 1*, 22 Figures, and 11 Tables throughout text)

Abstract

The study of subfossil remains of Chironomids and *Chaoborus* larvae proves that the profundal bottom fauna changed from a *Lauterbornia-Sergentia* community to a *Chironomus-Chaoborus* community during the postglacial time. This succession is attributed to an increasing oxygen depletion of the hypolimnion and an accumulation of nutritive substances in the sediment.

## Contents

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*) Translator's note: Plate I is not contained i[illegible] on hand.

## I. Introduction

The present paper describes the development of a taxocoenosis as it was traced back over a period of 10,000 years. The objects of investigation were the Chironomidae and the culicid Chaoborus flavicans* in the Schöhsee, a lake near Ploen, Schleswig-Holstein, Germany. The subfossorial material was recovered from four sediment cores picked up with a piston corer from the bottom of this lake.

Variations in the qualitative and quantitative composition of the fossil assemblage [thanatocoenosis] are documentative of changes in the taxocoenosis and furnish information as to the ecology and distributional history of the species. The interpretation of the observed changes will be attempted. This inevitably necessitates touching on the developmental history of the biotope. However, it is not the scope of this investigation to elucidate the lake's history on the basis of its Chironomidae successions; this problem would require inclusion of the chemical composition (which has already been determined) as well as additional fossils (diatoms, rhizopoda, cladocera, bryozoa). If distinct characteristics of the biotope are to be inferred from the fossorial Chironomidae and Chaoborus fauna, such inferences would have to be supported by additional investigations of that nature.

The prerequisites for a meaningful evaluation of the results are promising:

1. The sediment cores contain a cumulation of all deposits in the lake since its formation during the late glacial period. Thus, all historical phases of the biotope are represented. It is of importance that the sediments were dated with the help of the pollen analysis (SAAD

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*) Translator's note: Chaoborus is also known as Corethra; some investigators are more familiar with the latter generic name for this gnat. (Cf. ALLEE & SCHMIDT: Ecological Animal Geography; 2nd ed., 1951, p.392)

1966, 1970), and that the postglacial development of the climate in Central Europe is rather well known.

The Chironomidae inhabit the lakes with numerous species (e.g., Schöhsee = >100) which are, ecologically, vastly different. It is therefore to be expected that they react accordingly to fluctuations in the environmental factors. Such milieu changes manifest themselves not only negatively by the extinction of some species, but also positively in that the latter can be replaced by other species.

3. The discussion of environmental conditions is facilitated because the important ecological factors, particularly those prevailing in the profundal zone, can be corroborated. These are, in essence, temperature, oxygen supply, and food.

4. In order to procure valid results, they must be based on an utmost amount of material especially if frequency variations for individual taxa are to be determined. Previously published investigations have already shown that subfossorial remains of Chironomidae and Chaoborus larvae are to be expected in limnal sediments regularly and in large numbers.

5. At the outset, there was uncertainty about one last important requirement: It was doubtful whether the fossil remains would be p.3 identifiable to such a degree that they could be used for argumentation. As implied above, the ecology and developmental history of the Chironomidae is to be dealt with, and any discussion in relation to this is possible only on the basis of species. The identification of the subfossorial material will be the subject of a separate report.

Several previous publications already deal with subfossorial Chironomidae and Chaoboridae. These have been compiled and briefly reviewed by FREY (1964 : 70-77; cf. STAHL 1969). Besides the numerous reports about chance findings in the course of pollen analyses and other sediment examinations, there are several authors who concentrated especially on these particular subfossils: e.g., DEEVEY (1942), KONSTANTINOV (1951), STAHL (1959), BRYCE (1962). These investigations do not lend themselves to direct comparison with the present survey: In most cases, the sediments came from shallower inland waters, the deepest being the Linsley Pond (Connecticut) with 15 m (DEEVEY), and Myers Lake (Indiana) with 17 m (STAHL). The sample distances are considerably greater: STAHL and DEEVEY = about 1 m, KONSTANTINOV = 40-50 cm (at a core length of 2-3 m). Thereby, the material is rather limited. Furthermore, identification (with the exception of KONSTANTINOV) is not very detailed (genus or subfamily). The present investigation was concerned with a deep Baltic lake; two of the cores were taken from its profundal zone (22 m and 26 m). Sampling from the sediment cores was aimed at short distances (10 cm apart) so as to have an abundant material on hand (9,873 Chironomidae head capsules, 817 Chaoborus mandibles), and to facilitate detailed identification (49 Chironomidae taxa).

This work was performed under the guidance of Prof. Dr. J. ILLIES (Schlitz, Hesse, Germany), to whom I wish to express my thanks for assigning this interesting problem, for his valuable counsel, and for his continued support and encouragement. The core borings were part of an extensive sediment project supported by the "Deutsche Forschungsgemeinschaft" (German Research Society), and headed by Prof. Dr. W. OHLE. He very generously consented to the utilization of samples from the sediment cores, and I am grateful to him for the stimulating discussions about problems concerning limnal sediments.

## II. Characteristics of the Schöhsee

The Schöhsee is one of the numerous inland water reserves created by glacial ice and debris that characterize East Holstein as a landscape that was shaped under the influence of the ice age. With its surface area of 79 hectares, it is not one of the larger lakes. The water level stands at 22.5 m above NN*; maximal depth is 30.2 m, average depth 13 m (WEGEMANN 1922 : 23). The lake basin is divided into four parts by islets and shallows; the sediment cores investigated here come from the deepest points of these basin divisions.

The annual temperature range is marked by a typical summer stagnation with oxygen depletion below 15 m, and by homothermia during winter. p.4

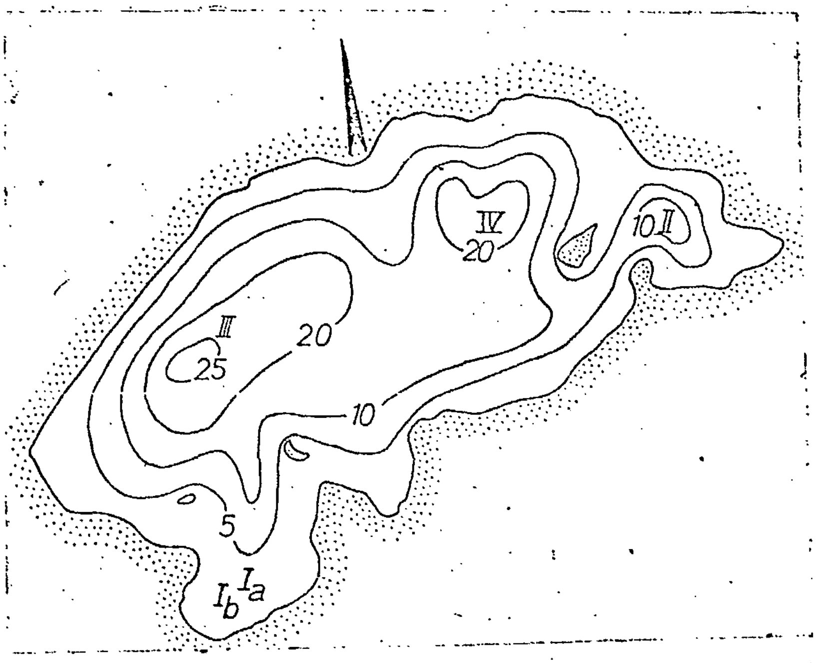

Fig. 1. Map of Schöhsee (I - IV = bore locations)

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*) Translator's note: NN: Normal Null = mean sea level, for West Germany the median watermark at the Amsterdam tide register.

The Schöhsee differs from neighbouring inland waters by the low calcium content of the water (31.9 mg Ca/liter as compared to 45.3 mg Ca/liter in Great Ploen Lake), and of the sediment (5.3% Ca of total sediment; Great Ploen Lake = 12.5% Ca of total sediment), as well as by its lesser production (OHLE 1934, 1952 : 249, 1964 : 415; UNGEMACH 1960 : 183-186). The sediment is markedly influenced by clay particles which are washed into the lake from an artificial embankment. UNGEMACH (*loc.cit.*) classifies it as mineral sediment.

For the determination of the pedonic fauna, 135 bottom samples were collected with [illegible] a dredge, and evaluated. In the sublittoral and upper profundal zones (depth 11-19 m) the average findings were: 190 Chironomidae, 1,500 *Chaoborus flavicans*, and 3,900 Tubificidae per square meter. In the lower profundal zone of the east basin (depth 20-22 m) there were 110 Chironomidae, 1,500 *Chaoborus* and 5,300 Tubificidae, in that of the west basin (depth 20-30 m) 40 Chironomidae, 3,100 *Chaoborus*, and 10,000 Tubificidae per square meter. This shows that the pedon is occupied to an overwhelming majority by *Chaoborus* and Tubificidae.

The most common Chironomidae species in the sublittoral and upper profundal zones were (in the order of their abundance): *Chironomus anthracinus*, *Chironomus plumosus*, *Monodiamesa bathyphila*, *Procladius* species, and *Polypedilum nubeculosum*. In the lower profundal zone, these were: *Polypedilum nubeculosum*, *Chironomus anthracinus*, *Calopsectra* and *Tanytarsus*. In the first-mentioned zones, the two *Chironomus* species represent more p.5 than 40% of the stores, whereas, in the lower zone, the dominant species is *Polypedilum nubeculosum* with a relative abundance of 40%. Thus, the

Chironomidae fauna of the profundal zone is characterized by a peculiar composition of species, and by an extremely low population density.

## III. Methods

For the underwater borings, a LIVINGSTONE piston sampler (LIVINGSTONE 1955 : 137-139) was utilized with appreciable success. To ensure drill-stem navigation of utmost precision, a guideway tube-casing was employed. The piston and the arresting gear were constructed according to Prof. OHLE's specifications (SAAD 1966 : 5-6).

With the LIVINGSTONE piston corer, whose cutting tubes are 1.20 m long, sediment cores measuring 1 m in length are picked up.

In order to obtain a good collective sample of the top 40 cm of sediment, and to have a larger material from this layer at our disposal, a sludge hoist [or dredge] according to OHLE was employed.

The depth of the lake was 12 m at bore location I, 10 m at bore location II, 26 m at bore location III, and 22 m at bore location IV, so that the sediment profiles of I and II represent the sublittoral zone, and those of III and IV reflect the profundal zone, even considering the postglacial fluctuations of the lake's water level (cf. Table 1, p.11).

For sampling, the sediment cores were pressed out of the cutting tubes and carved up (SAAD 1966 : 7, and Figs. 6 and 7). In general, the random samples (about 5-10 ml of sediment) were taken 10 cm apart from one another; where closer layering was visible, correspondingly shorter distances were chosen. In this connection, it should be pointed out that sampling distances of 10 cm proved sufficient throughout, except in pollen zones with a very low sediment saturation (pollen zones IV, V, VI, and VII), where shorter intervals would have been preferable because, often, only two or three samples were available from these zones. Regrettably, there was no way of anticipating how the pollen analysis would turn out. The fresh mud samples were stored, without prior preservative treatment, in jars with snap-on covers.

Before the sediment samples can be scanned for Chironomidae head capsules and Chaoborus mandibles, preparatory measures have to be taken for two reasons: In the first place, because the chitinous remains have to be freed from the fine detritus of the mud, so that they become distinguishable, and secondly, the volume of the samples to be investigated must be reduced, without loss of microfossils, to an absolute minimum in order to keep the workload involved in isolating the head capsules and mandibles within reasonable limits.

For the preparation of sediment samples prior to microfossorial analysis, a host of instructions are offered in the literature: DEEVEY (1942 : 239-241, 1955 : 295), KONSTANTINOV (1951), LIVINGSTONE et al. (1958 : 193), STAHL (1959 : 49-50), BRYCE (1962). In principle, the methods are all very similar and differ in detail only. Based on directions from the literature and on our own experience, the following simple and time-saving method was designed for our investigations:

In an Erlenmeyer flask (capacity 50 ml), one ml of sediment — measured with a calibrated glass or plastic cylinder (SAAD 1966) — together with 15 ml of a 10% potassium-hydroxide solution is boiled in a water bath for 10 minutes. The sample is then diluted by filling up with water, allowed to cool slightly, and poured through a plastic sieve (mesh width 0.132 mm). With a dosed water jet, even the fine sediment is rinsed out. The sieve with the residue is placed in a shallow dish containing p. 6

a 10% HCl-solution (especially important when sediments are very rich in calcium); after foaming has subsided, the sample is once more washed thoroughly. The remainder is then rinsed from the sieve into a beaker, using a plastic spray bottle, and finally poured into a centrifugal flask. It takes one hour at the most until the sample has settled — centrifugation is then not necessary — and the supernatant water is decanted. The precipitate is placed for investigation onto a gridded slide, picking up small portions at a time with a pipette, and examined under a binocular microscope at a magnification of X 25 to 40.

Since permanent slides were to be prepared of all Chironomidae and Chaoborus remains, the latter were collected with fine needles and pincettes, placed briefly into a small receptacle containing 96% alcohol, then removed, embedded in "Euparal" (Chroma-Gesellschaft, No. 30440), and finally mounted on slides in such a manner that the ventral side of the Chironomidae head capsules was orientated upward (cf. SCHLEE 1966 : 188-189).

The relative humic acid concentration was determined of all samples from Schöhsee-core III, and of a few samples from the core obtained in Great Ploen Lake. The method employed represents a combination of those described by OVERBECK & SCHNEIDER (1940 : 340-347) and UNGEMACH (1960 : 302-304): The sediment sample was dried at 95°C; 200 mg of the dry substance, weighed into 100 ml of 0.5% NaOH, was boiled for one hour, then filled up with aqua dest. to 200 ml, and cooled for several minutes. After filtering (Schleicher & Schüll filter No. $589^3$), the extinction coefficient of the filtrate was measured immediately with a photometer (filter: S 38; cuvette: 0.5). The readings were related to a layer thickness of 1 cm.

## IV. Dating of sediments

SAAD (1966 : 18-26) performed the pollen analyses of sediment cores I, II, III, and the lower part of core IV. The pollen zones correspond to those decided on by OVERBECK & SCHNEIDER (1938) and by SCHMITZ (1953). Therefore, the time of deposition is known for each sediment sample. This circumstance is of great importance in our investigation, indeed, it is thereby that a meaningful evaluation of the results becomes possible.

The periods of the postglacial climate and forest history in Central Europe during the span of time that is of interest here, have been compiled in Table 1.* It also denotes the meaning of the symbols used in the diagrams to indicate the individual pollen zones. For most of the pollen zones, two different years are mentioned under "absolute dating" which means that the absolute dates arrived at with the help of the $^{14}$C-method are cumulative in this particular range (according to STRAKA 1961). The data on postglacial fluctuations in the water level of the lake are cited from the works by GRIPP (1953), NILSSON (1964), and KONDRACKI et al. (1965).

## V. Biocoenosis -- thanatocoenosis

p.7

"Biocoenosis and Thanatocoenosis" is the title of WASMUND's (1926) "biosociological study of life assemblages and death assemblages" (cf. BOUCOT 1953). The step to be taken is that from the recovered head capsule — deposited at a certain time in a certain place — to the chironomid larva which, ages ago, shed its exoskeleton somewhere in the lake; it is the step from the recovered assemblage of Chironomidae head capsules (thanatocoenosis) of a sediment sample to the taxocoenosis (SCHÖNBORN 1967 : 185) which left these remains behind.

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*) For Table 1 see next page (p.11)

Table 1

Postglacial history of forests and climate in Central Europe

[The "absolute" dates (after STRAKA 1961) are — according to recent dendrological studies — certainly in need of correction.]

| Pollen zone | Absolute dating | Climate (stage) | Characteristic forest formation | Water-level fluctuations |
|---|---|---|---|---|
| XII | 1300 | Subatlantic II | beeches | rising (not reaching level of Atlantic stage) |
| XI | -1200/0 | Subatlantic I | oaks/beeches | |
| X | -1100/700 | Subboreal II | oaks | low (about 4 m below level of Atlantic stage) |
| IX | -3000 | Subboreal I | oaks/hazel trees | |
| VIII | -6200/5500 | Atlantic | oaks/mixed forest /hazel trees | high |
| VII | -7100/6800 | Boreal II | pine/hazel | low |
| VI | -7700/7500 | Boreal I | pine trees | high |
| V | -8500/8200 | Preboreal | birch trees | high |
| IV | -9300/8900 | later Dryas<br>" Subarctic | later period of birch/park-tundras | high (5 m above present level) |

An important question in the evaluation of a thanatocoenosis is that regarding the origin of the fossils. In the case of the Chironomidae head capsules, the answer is simple: The larva lives in the mud of the profundal zone (mostly in mud tunnels), where it sheds its exoskeleton four times; the exuviae remain right there, forming part of the sediment proper. Thus, the Chironomidae thanatocoenoses are identical with the necrocoenoses as discussed by STEINECKE (1927; cf. WASMUND 1929 : 490): The thanatotope equals the biotope; this concept greatly facilitates the interpretation of the thanatocoenoses (cf. GROSPIETSCH 1954 : 96). In fact, in the course of our investigations (as should be mentioned beforehand) it turned out that the thanatocoenosis of a sublittoral or profundal sediment does not contain a mixture of Chironomidae remains from the entire lake, but that it is representative only of assemblages in the stratum from which the sample was obtained. p.8

WASMUND (1929:491) considers the necrocoenoses in any case as "distorted documents" because not all species were equally resistant against bacterial decomposition; instead, a selection of less destructible forms would take place. Therefore, findings based on the necrocoenosis would furnish a wrong picture of the composition of the former taxocoenosis. For the destruction of head capsules, chitin-decomposing bacteria would have to be present. In fact, such bacteria exist in inland waters in great numbers: RUSCHKE & RATH (1967) were able to isolate from the water of lakes Feldsee and Titisee 14 strains of bacteria capable of attacking chitin. The authors used chitin powder in their experiments. KRAUSE (1962) investigated the bacterial decomposition of copepoda and cladocera plankton. This work resulted in the identification of two chitin fractions (loc. cit., pp.79-80), one of which is easily decomposable (e.g., shell fragments, fragments of biramous antennae, postabdomina, and the filter combs from the extremities of _Daphnia_; the rostrula of _Bosmina_). DEEVEY (1964) established that the chitinous remains of diaptomid copepoda are already being decomposed while they are sinking; although the cyclopoid copepoda, rotifera, and dinoflagellata do first reach the bottom, they are then also rapidly decomposed. On the other hand, _Bosmina_ and the Chydoridae are quantitatively preserved in form of their bivalve shells. _Bosmina_ is, according to DEEVEY (loc. cit.), overrepresented because of its frequent moldings which produce numerous exuviae.

Chironomidae head capsules (as well as the mandibles of _Chaoborus_) have a much more robust structure than, for example, the outer integument of the cladocera. The chitin layers are thicker and, in most instances, sclerosed. KRAUSE (1962 : 78-79) points out that the rapid decomposition of chitin from crustacean plankton is due to the fact that chitinolysis can set about "universally, starting with minute and usually also very thin-walled chitin structures", and that "size and and surface structure of the objects play, without doubt, a decisive role in determining the speed with which decomposition progresses."

It appears that the chitin of Chironomidae head capsules — except perhaps for those from the first larval stage — are not attacked at all: Even very fine structures like the pinnate inner seta of the mandible, and other minute setae of the labrum and trophi are well preserved in specimens from the youngest to the oldest layers, as far as they had not broken away.

To infer from the degree of resistance with which chitin resists bacterial decomposition that the thanatocoenosis completely equals the corresponding taxocoenosis requires several additional considerations:

1. Only three head capsules per larva can be taken into account since four metamorphoses take place, but the tiny, delicate head capsule from the first larval stage (larvule) is always destroyed (Fig. 2, p. 14) by bacteria or by mechanical means, and would anyway pass the sieve unnoticed p. 9 (cf. STAHL 1959 : 81-84).

2. It is true that the exoskeletons of larvae inhabiting the deepest spots of the lake basin are sedimented in their habitat, but this does not necessarily apply to larvae living in the littoral and sublittoral zones. On the contrary, as a rule, no sedimentation whatsoever takes

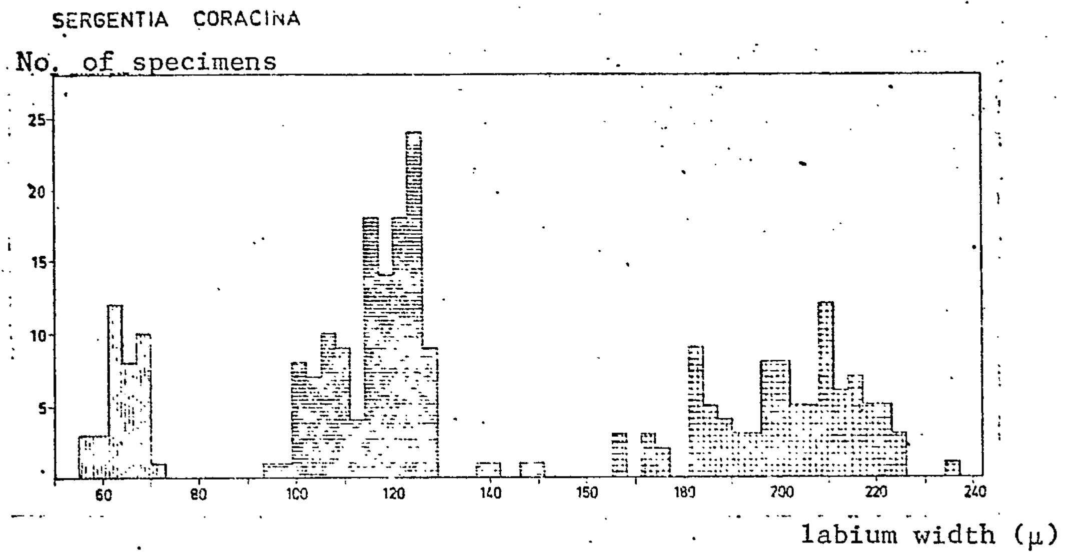

Fig. 2: *Sergentia coracina*; size-frequency distribution of 261 head capsules.

place in the littoral zone; instead, the suspended detritus is transported to the sublittoral and profundal zones for final deposition.

The fact that a limited number of the head capsules found in profundal sediments belong to obligate stenobathic communities (e.g., *Cricotopus*, *Paratanytarsus*, *Psectrocladius*, and *Glyptotendipes*) demonstrates the considerable influence exerted by the littoral zone on the profundal sediments.

The stenobathic communities of the littoral zone can, in most cases, be easily identified as allochthonous elements. However, other taxa such as *Dicrotendipes*, *Polypedilum*, *Microtendipes*, *Procladius*, cannot be assigned as readily to a certain level of depth.

It can also be assumed that exoskeletons from adjacent, only slightly higher, regions are transported into the hollows and, while hardly influencing the qualitative composition of the thanatocoenosis, increase the fossil density. It is to be expected, therefore, that the head capsules are concentrated in the deepest spots of the lake basin.

This also explains why calculations, based on fossil distribution and estimated sedimentation rate, result in very high values for the former population density. For example, in core III (6.80 m long) an average of 1,428 head capsules per $cm^2$ were deposited annually if the sedimentation period is estimated as having been 10,000 years (cf. STAHL 1959 : 86-89). Asssuming furthermore that the life cycle of all the species had been one year, this would then correspond to a mean population density of about 3,600 individuals per square meter. For core I, one would arrive at 4,500, and for core IV even at 5,800 individuals per square meter. p.10

It is of great advantage if, as in our case, the cores come from maximal depths of more or less secluded basins: Although the sediments are influenced by the shallower parts of the respective lake region, they themselves are not subject to shifting into greater depths and are, therefore, not attenuated. It is of importance also that borings from the sublittoral and profundal zones can be compared with one another because this is the only way to establish the depth zone in which a species had its optimum.

3. Another source of error lies in the possibility that not all of the larval exoskeletons are deposited in the same place in which the larva lives. Apart from the fact that the head capsules of larvules have never been recovered as fossils, there are also some species (e.g., Chironomus) whose last larval exoskeleton stays with the pupal case. This coarctate floats to the surface and, after eclosion, the last exoskeleton is thus blown ashore by the wind together with the pupal case. This type of larva leaves not four but only three larval heads behind in the thanatope; of these, only two (2nd and 3rd stage) can be recovered with the

method employed here. If the head capsule from the last larval stage of a Chironomidae species is always lost in this manner, this species is underrepresented in the thanatocoenosis by 33%.

4. Finally, it also makes a difference whether a species has a life cycle of one or of two years, or whether it produces even several generations within a year, because the number of larval exoskeletons produced annually depends upon this factor.

While points 1-3 do not carry too much weight in the discussion of relative variations, more importance is attached to the last-mentioned. The number of generations per year differs not only from species to species, but can be subject to changes even within a species, depending upon prevailing climatic conditions. An adaptive change from a two-year to a one-year life cycle would have its reflection in the thanatocoenosis on account of the relative increase in the number of exoskeletons and, thus, simulate an increased population density. Besides, confirmed biennial species like Chironomus rempeli (REMPEL 1936) and Sergentia coracina, Titisee (WÜLKER 1961 : 318-323) are, in comparison with the annual species, underrepresented in the necrocoenosis.

The following is valid only with the above-mentioned reservations: The Chironomidae and Chaoborus necrocoenoses of the investigated sublittoral and profundal sediments are proportional to the corresponding taxocoenoses.

## VI. Significance of results

The Chironomidae head capsules and Chaoborus mandibles were recovered from each random sample by quantitative selection from 1 ml of fresh sediment. Thus, the first value obtained is that of fossil density p. 11

(specimens/ml of sediment) which is then itemized according to individual taxa.

The following test shows how each of the values, derived from 1 ml sediment per sample, is to be analyzed: From one sediment layer of core III (1.70 m), ten samples of 1 ml sediment each were collected, and tested separately. The results are shown in Table 2.

Table 2: Number of Chironomidae head capsules and Chaoborus mandibles per ml of sediment, recovered from ten random samples (a-j) of the same horizon (core III, 170 cm).

Ø = mean number of head capsules

C = constance (number of species-positive samples expressed as percentage of the total number of samples

| Taxa | Random samples | | | | | | | | | | Total | Ø | C |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | a | b | c | d | e | f | g | h | i | j | a—j | | (%) |
| *Procladius* | 1 | | 2 | 2 | 3 | 4 | 2 | 1 | 1 | 4 | 20 | 2,0 | 90 |
| *Labrundinia longip.* | | | | | | | 1 | | | 1 | 2 | 0,2 | 20 |
| Pentaneurini | 4 | 1 | | 1 | 1 | 1 | | | 3 | 1 | 12 | 1,2 | 70 |
| *Cricotopus* A | 2 | | | 1 | | | 2 | 1 | 4 | | 10 | 1,0 | 50 |
| *Psectrocladius* | 2 | | | | 1 | | | 1 | 1 | 1 | 6 | 0,6 | 50 |
| *Parakieff. bathophila* | | | | 1 | | | | | | | 1 | 0,1 | 10 |
| Orthocl. gen? *triquetra* | | | 1 | 2 | | 1 | 1 | 1 | 1 | 2 | 9 | 0,9 | 70 |
| *Chironomus* | 5 | 1 | 2 | 1 | 3 | 4 | 1 | 3 | | 1 | 21 | 2,1 | 90 |
| *Glyptotendipes* | | | | | | | | | 1 | | 1 | 0,1 | 10 |
| *Limnochironomus* | | | | | 2 | 2 | 1 | | | 2 | 7 | 0,7 | 40 |
| *Parachironomus* | | | | | | | | | | 1 | 1 | 0,1 | 10 |
| *Cryptocladopelma* | 1 | | | | | | 1 | | | | 2 | 0,2 | 20 |
| *Stictochironomus* | | | 1 | | | | | | | | 1 | 0,1 | 10 |
| *Polypedilum* | | | | | | | 1 | | | | 1 | 0,1 | 10 |
| *Lenzia* | | | | | | | | | | 1 | 1 | 0,1 | 10 |
| *Sergentia coracina* | 4 | 3 | 3 | 3 | 1 | 3 | | 4 | 1 | 3 | 25 | 2,5 | 90 |
| *Microtendipes* | 1 | | | 1 | | | 1 | | 1 | 2 | 6 | 0,6 | 50 |
| *Paratendipes* | | | | 1 | | | | | | | 1 | 0,1 | 10 |
| *Calopsectra* part. | 1 | 3 | 2 | 2 | 2 | 2 | 4 | | 6 | 6 | 28 | 2,8 | 90 |
| *Tanyt. heusd.*-Kreis | | | | | | | | | | 1 | 1 | 0,1 | 10 |
| *Tanytarsus* B | 1 | | | | | | | | | | 1 | 0,1 | 10 |
| *Tanytarsus* C | 2 | | 2 | | | | | | 1 | 1 | 6 | 0,6 | 40 |
| *Corynocera ambigua* | 4 | | | | | | 1 | 1 | 3 | | 9 | 0,9 | 40 |
| *Tanytarsus* part. | 10 | 2 | 3 | 3 | 5 | 7 | 6 | 5 | 11 | 10 | 62 | 6,2 | 100 |
| *Paratanytarsus* | | | | 1 | 2 | 1 | | 2 | 2 | 1 | 9 | 0,9 | 60 |
| *Cladotanytarsus* | 1 | 2 | | 1 | 1 | | 1 | 2 | 4 | 2 | 14 | 1,4 | 80 |
| *Stempellina* | | | | | | | | | | 1 | 1 | 0,1 | 10 |
| *Stempellinella* | | | | | | | | | 2 | | 2 | 0,2 | 10 |
| *Thienemanniola* | | | 2 | | 1 | | | | 2 | | 5 | 0,5 | 30 |
| Chironomidae | 39 | 12 | 18 | 20 | 22 | 25 | 23 | 21 | 44 | 42* | 266* | 26,6* | 100 |
| *Chaoborus flavicans* | 12 | 3 | 7 | 4 | 10 | 9 | 12 | 10 | 12 | 17 | 96 | 9,6 | 100 |

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*) Translator's note: These three figures should correctly read: 41 / 265 / 26.5

What comes first to light in this test is the important fact that the number of Chironomidae head capsules per ml of sediment can vary considerably from sample to sample of this seemingly homogeneous material. The mean value lies at 27 specimens/ml, but individual values fluctuate between 44 and 12 specimens/ml. Therefore, in quantitative evaluations, single random samples must not be overrated.

The standard deviation from the mean, $s_X$, to which the formula p. 12

$$s_x = \pm \sqrt{\frac{\Sigma(x_i - \bar{x})^2}{n(n-1)}}$$

applies, amounts for the Chironomidae head capsules (mean = 26.6 specimens/ml) to ± 3.4, and for the Chaoborus mandibles (mean = 9.6 specimens/ml) to ± 1.3; that is to say, the standard deviation is very low.

If a great number of samples would be taken from each sediment layer, significant quantitative variations could be established also in adjacent samples. However, this would entail an enormous work load which is not warranted by the anticipated results. When even those changes that occur over a long period of time are difficult to interpret (as we shall see), such short-term events evade interpretation altogether: It is hardly possible to explain the exceptional fossil density in single samples, as in that from the 8.50 m horizon of core IV, and definitely also in the samples from the 4.81 m horizon of core IV, and the 3.63 m horizon of core III, without resorting to speculation. Only large-scale changes as they reflect against the background of postglacial climates lend themselves for discussion.

Another fact clearly emerges from Table 2 (p.14), namely the constancy with which individual species occur in the ten random samples. The most frequent taxa, Tanytarsus part. and Chaoborus flavicans, which are represented with a total mean of 6.2 and 9.6 specimens, did show up also in all single samples. Taxa with an expected total mean of 2.0 to 2.8 specimens are present in nine of the ten random samples: Procladius, Chironomus, Sergentia coracina, and Calopsectra. In five to eight samples, there were three forms with a total mean of only 1.0 to 1.4 specimens (Cricotopus, Pentaneurini part., Cladotanytarsus). Generally, the following applies: If a sample contains an average of 27 head capsules per ml of sediment, it can be expected that the taxa represented by one or more specimens will be recovered also from two or three adjacent random samples. These samples, taken at 10 cm intervals, give an accurate picture of the Chironomidae necrocoenosis encountered in a homogeneous sediment column measuring 30 cm in length. As can be seen from Table 2, in addition to the abovementioned frequent taxa, there are also 21 types which are represented by less than 1 specimen, according to the calculated mean; nine of these species contribute only a single specimen to the total number of 266 head capsules. It is among these that quite a number can be labeled as obligate stenobathic organisms, and their remains came probably into this profundal sediment on a secondary basis; these are: Glyptotendipes, Lenzia, Parachironomus, Paratendipes, Stictochironomus, Tanytarsus B, Tanytarsus heusdensis group ("Kreis"). These as well as the slightly higher represen- p. 13 ted species made quite an irregular appearance in the samples and were detected more or less by chance. Even an isolated occurrence of such a rare species is proof of its presence in the lake during the corresponding period of time, but it does not necessarily follow that constant absence even from a number of samples may be interpreted as unequivocal evidence that the species no longer inhabited the lake at that time.

In the course of interpreting the results, reference will be made to the climatic periods. For this purpose, all individual samples belonging to the same climatic period were combined and their mean value was used for quantitative evaluation. In other words, the calculations are not based on individual but on mixed samples consisting of a varying number of random samples.

However, the mean values need rechecking so as to verify that they reflect the situation correctly: The single random samples will reveal whether these are really in close vicinity of the calculated means, or whether they are indicative of quantitative changes within the climatic period. It is also possible that the mean value is very strongly influenced by a single, markedly diverging, sample.

The total number of Chironomidae head capsules and Chaoborus mandibles is expressed as the mean abundance (specimens/ml) per climatic period.

Since this absolute abundance fluctuates considerably (as shown in Fig. 3, p.22), the mean of the relative abundance is of much greater assistance in comparative studies of individual Chironomidae taxa. However, meaningful values result only for the more frequent species. For rare species, the number of specimens recovered is all that can be entered.

The relative abundance indicates what share a species has in the mean value of the necrocoenosis of a given climatic period. Changes in these values in the course of time illustrate the developmental dynamics of the Chironomidae populations: It becomes manifest that the dominant species become more and more rare until they finally disappear and new species take their place; it can also be seen at a glance that other

Chironomidae migrate at a certain time from the sublittoral into the profundal zone.

## VII. Distribution of the subfossils throughout the sediment cores

### A. Total number of head capsules

Core I (Figs. 3, p.22, and 4, p.27)

Of core I, which was 7.25 m long, 94 random samples of 1 ml each were collected from 68 horizons and analyzed. A total of 2,860 head capsules was recovered from these samples. As is shown in Figs. 3 and 4, instead of being evenly distributed throughout the sediment layers, the number of head capsules varies greatly from one volume unit to the other.

Chironomidae head capsules and other limnetic fossils (e.g., cladocera-remains) are abundantly present even in the lowermost layers. The amount of head capsules shows an initial increase during the later Dryas stage until it reaches a maximum (81 specimens/ml at 695 cm horizon); it then decreases toward the Preboreal. In pollen zone IV, the mean value (36 specimens/ml) is about three times higher than in zone V (13 specimens/ml). In the deposits then following during Boreal I (pollen zone VI) the values remain about stable, but show a marked decline during Boreal II and the Atlantic stage; here, fossil density is at a minimum (6 and 5 specimens/ml respectively). However, this makes the enormous increase which commences at the borderline of pollen zone VIII/IX all the more meaningful. Maximal amounts are found in Subboreal I: 145 specimens/ml at the 160 cm horizon, 164 specimens at 150 cm, and 184 specimens at 200 cm. The mean value for this climatic period (78 specimens/ml) is correspondingly high; it is the highest of all the means calculated in the course of this investigation. Fossil density then declines significantly at the transition p.15

p. 14

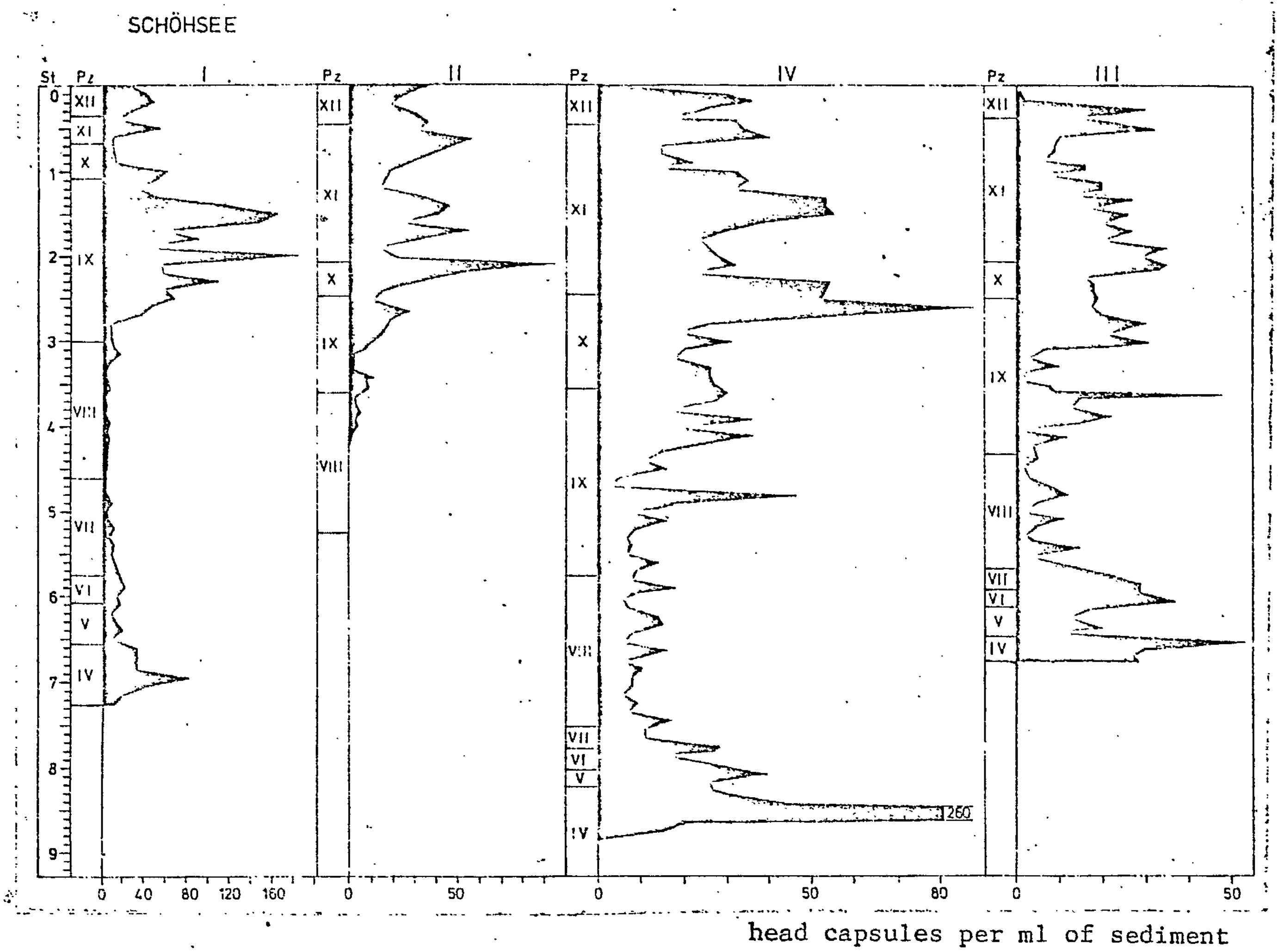

Fig. 3: Schöhsee, cores I-IV; number of Chironomidae head capsules per ml of sediment in individual samples (Pz = pollen zone; St = depth of mud, expressed in meters).

p. 15
cont'

to the next zone: The mean value for Subboreal II amounts to a mere 12 specimens/ml, for Subatlantic I it is 34 specimens/ml. The samples investigated from pollen zone XII consisted of 4 to 5 ml of sediment so that, here, also individual values are statistically well secured. Initially, there is an increase: At 30 cm = 26 specimens/ml; 20 cm = 46 specimens/ml; 10 cm = 41 specimens/ml; then, at 1 cm, they decrease to 29 specimens/ml.

Core II (Figs. 3, p.22, and 4, p.27)

Random samples were collected from 48 horizons of core II which had a length of 5.20 m. In total, 1,317 head capsules were recovered.

The oldest sediments of core II were deposited during the Atlantic stage (pollen zone VIII), that is, they are considerably younger than the oldest sediments of the other cores. In the horizon between 4.20 m and 5.20 m there were no limnetic fossils found. According to SAAD (1966), this sediment contains practically no organic substances. It is therefore unlikely that we are dealing here with the deposits of a lake. Thus, the limnetic sediment has only a thickness of 4.10 m.

The number of head capsules from the Atlantic stage is minimal: An average of 4 specimens/ml. With 11 specimens/ml, the mean fossil density of Subboreal I is not much higher; however, a distinct increase in the values can be observed in Table 2 (p.17). The maximum is reached during Subboreal II with 46 specimens/ml; here was also the highest single value established: 95 specimens/ml at a depth of 2.10 m. The numbers recovered from the individual samples of Subatlantic I fluctuate considerably, namely between 14 and 56 specimens/ml. However, since adjacent samples account for values of similar magnitude (1.01m—1.20m = 15-19 specimens/ml; 1.30m—1.50m = 35-41 specimens/ml), it must be assumed that these variations are significant, and not due to insufficient sample plotting. The mean fossil density in this zone is 32 specimens/ml. It remains about the same in the youngest sediments (30 specimens/ml). The individual values for Subatlantic II represent the means of several random samples and can thus be considered as statistically secured; they reveal an initial decrease in fossil density, followed again by an increase during the very last developmental phase.

Core III (Figs. 3, p.22, and 4, p.27)

A total of 121 random samples collected from 80 horizons were investigated of core III, which was 6.80 m long. In all, 2,075 head capsules were recovered.

The oldest layers, which accumulated during the later Subarctic period, contain Chironomidae fragments and other limnetic fossils in considerable numbers. The 53 head capsules per ml from the 6.54 m horizon constitute even the highest single value of the entire core. The mean from the later Dryas stage amounts to 35 specimens/ml. The values decline distinctly at the border toward the Preboreal (mean in zone V = 15 specimens/ml), but increase again at the transition to Boreal I, so that the mean value for Boreal I is again 33 specimens/ml. This standard is fairly evenly retained throughout the following layers (Boreal II = 26 specimens per ml). However, during the Atlantic stage, the number of specimens/ml is very low; the mean value is the lowest of the entire core: 6 specimens/ml. The distribution during Subboreal I reveals three divisions: High frequencies in the earliest and latest third, low frequency in the intermediate third. The average lies at 15 specimens/ml. At the border toward Subboreal II there is no change in fossil density, but the centre of this zone shows significantly increased values: the mean is 24 specimens/ml. The fossil content of Subatlantic I also shows distinct changes. It is high in the lower layers, but then decreases steadily in upward direction, and increases again during the last third. The mean value for the entire period amounts to 21 specimens/ml. The transition from zone XI to zone XII is marked by a very low value (which represents the mean from 4-7 random samples, as do all individual values of zone XII, so that they are well secured). The fossil density shows, at first, a marked increase in upward direction, but it is minimal in the two uppermost samples (0.17 m and 0.07 m); here, one ml of sediment contains only an average of 1-2 head capsules.

Core IV (Figs. 3, p.22, and 4, p.27)

Core IV had a length of 9.35 m; the segment between 8.80 m and 9.35 m did not consist of limnal sediments, but of detrital marl. Of these sediments, 147 random samples collected from 98 horizons were investigated. The material thus recovered consists of 3,721 Chironomidae head capsules.

The first Chironomidae-remains appeared in the 8.73 m horizon. They were deposited during the later Dryas stage (pollen zone IV). The most remarkable feature concerning the samples from this zone is the high fossil density of the sediment layer at 8.50 m: At 8.63 m, 19 head capsules were found; at 8.40 m, there were 44; but in-between, at 8.50 m, there were 260 specimens/ml! This is the highest number ever found during these investigations. Surprising is not only this large amount of head capsules, but also the fact that the values of both adjacent samples are so much lower. The result for pollen zone IV is strongly influenced by this one sample: The mean value amounts to 66 specimens/ml. p.17

The fossil concentration decreases steadily in the direction of the younger layers up to the Atlantic stage; the mean values are: Preboreal = 32, Boreal I = 23, Boreal II = 18, Atlantic stage = 10 specimens/ml.

Unfortunately, the pollen analyses performed by SAAD (1966) covered only the lower portion of this core. He did not determine the demarcation of zones VIII/IX, nor any of the younger zones. Since this would have made it impossible to compare conditions here with those in the other three sediment cores, an attempt was made to establish the borderlines between pollen zones in some other way. For this, the missing pollen profile was substituted with the Chironomidae diagram. The diagram of the profundal core III was used for comparison, and the possibility of synchronizing the diagrams of cores III and IV was examined. This method is bound to lack a sound basis. The reason for employing it just the same is the astonishing homogeneity over long stretches of both these diagrams. This similarity manifests itself most strongly during Subboreal I: One is almost compelled to relate the peak at 3.63 m in core III to that at 4.81 m in core IV. High and low values are grouped with amazing conformity during the following zone! Things become somewhat more difficult mainly during Subatlantic I because, here, the diagrams are very different after all. By contrast, the border towards Subatlantic II is very well demarcated by a minimum.

The similarity of the diagrams from cores III and IV is at the same time good evidence that even those values that are based merely on a single random sample, can nevertheless reflect the actual situation quite well.

After the minimum during the Atlantic stage, the Chironomidae fossil content increases again: Subboreal I = 18 specimens/ml; Subboreal II = 35 specimens/ml; Subatlantic I = 34 specimens/ml. During the most recent stage, the mean value becomes smaller again: Subatlantic II = 25 specimens/ml. Thus, the profile is in general similar to that obtained from the other profundal core, although the values from the Atlantic stage until Subatlantic II are here distinctly higher than in core III.

Comparisons between cores I-IV (Fig. 4)

With regard to the frequency distribution of head capsules in their sediments, the four cores are in many respects in agreement with one another: Sediments from the later Dryas stage are, throughout, characterized by high values (in cores III and IV, these are higher than in all other pollen zones). Fossil density then declines steadily until it reaches the smallest value during the Atlantic stage. Cores I and III correspond insofar as the Preboreal value is lower than that of Boreal I.

During the time from Subboreal I to Subatlantic II, only the sediments of profiles II, III, and IV are similar. The number of head capsules per volume-unit increases, reaches its peak during Subboreal II, and finally decreases again. The resulting general picture is therefore as follows: High values during the later Dryas stage, declining values until Atlantic stage, increase until Subboreal II, and again decrease until Subatlantic II. p. 18

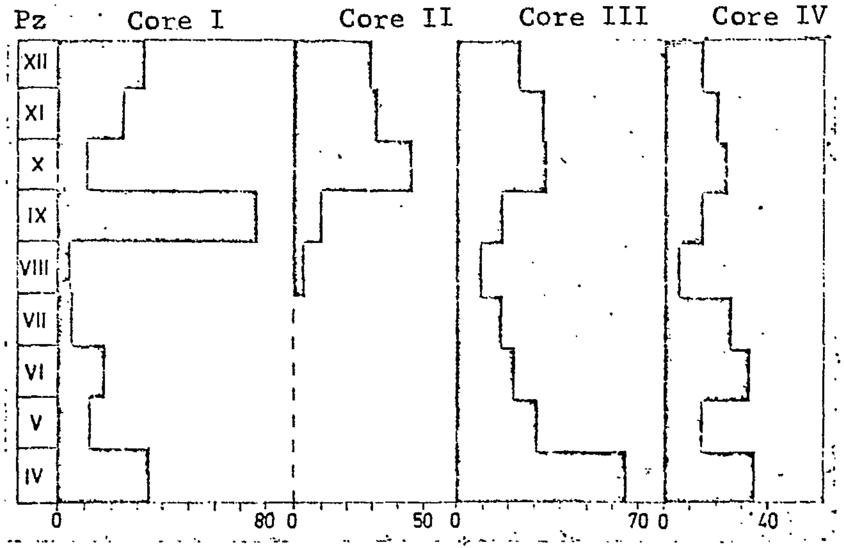

Fig. 4: Schöhsee, cores I-IV; Chironomidae head capsules per ml of sediment (mean values of climatic stages). Pz = pollen zone

Core I shows considerable deviation from this profile in its younger layers: Here, the maximum occurs already during Subboreal I. By contrast, Subboreal II is characterized by a particularly low value, and toward Subatlantic II, the frequency of head capsules is once more distinctly higher.

The number of head capsules per ml of sediment has the lowest collective mean in core III (21 specimens/ml), and the highest in core IV (29 specimens/ml). Cores I and II lie between these values with 25 specimens/ml each.

## B. The individual taxa

In total, 9,873 head capsules were collected from the sediment cores of the Schöhsee. The individual amounts for each of the taxa found in this material are listed in Table 3 (p.29).

A mere 6 of the 49 taxa make up 53% of the total number: Procladius, Chironomus, Calopsectra part., Corynocera ambigua, Lauterbornia coracina, and Tanytarsus part.

30 of the 49 taxa make up less than 1% and constitute together only 8.8% of the entire material. p.20

* More than half of the specimens belong to the tanytarsini, almost 80% to the Chironominae. The Tanypodinae constitute about 10%, and the Orthocladiinae barely 9%. 1.7% of the head capsules were unidentifiable because they were not well enough preserved; some of these were not classified also because they belonged to terrestrial forms.

The composition of the entire material was compiled only for the purpose of orientation about the frequency distribution of the 49 taxa.

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*) Translator's note: The percentages given in this paragraph do not tally with the total percentage of 100% which is indicated at the very bottom of Table 3; neither do the percentages reported in this Table add up the to indicated total of 100.0 (see p.29).

Table 3: Frequency distribution of Chironomidae taxa in the entire material from the four borings of the Schöhsee. (N = Number of head capsules recovered; % = relative frequency)

(on p. 19

| | N | % |
|---|---|---|
| 1. *Tanytarsus* v. d. WULP s. str. part. | 1 746 | 17,5 |
| 2. *Calopsectra* KIEFFER part. | 949 | 9,5 |
| 3. *Chironomus* MEIGEN | 758 | 7,6 |
| 4. *Procladius* SKUSE | 710 | 7,1 |
| 5. *Corynocera ambigua* ZETTERSTEDT | 619 | 6,2 |
| 6. *Lauterbornia coracina* KIEFFER | 497 | 5,0 |
| 7. *Microtendipes* KIEFFER | 469 | 4,7 |
| 8. *Sergentia coracina* ZETTERSTEDT | 427 | 4,3 |
| 9. *Cladotanytarsus* (KIEFFER) KRÜGER | 403 | 4,0 |
| 10. *Cricotopus* (v. d. WULP) EDWARDS A | 391 | 3,9 |
| 11. *Pentaneurini* (FITTKAU) part. | 292 | 2,9 |
| 12. *Thienemanniola* KIEFFER | 284 | 2,8 |
| 13. *Paratanytarsus* (BAUSE) KIEFFER | 257 | 2,6 |
| 14. *Dicrotendipes* KIEFFER | 240 | 2,4 |
| 15. *Cryptocladopelma* LENZ | 227 | 2,3 |
| 16. *Polypedilum* KIEFFER | 157 | 1,6 |
| 17. *Psectrocladius* (KIEFFER) EDWARDS | 147 | 1,5 |
| 18. *Tanytarsus* v. d. WULP s. str. B | 118 | 1,2 |
| 19. *Tanytarsus heusdensis*-Kreis (THIENEMANN) | 116 | 1,2 |
| 20. *Pseudochironomus* STAEGER | 92 | 0,92 |
| 21. *Parakiefferiella bathophila* KIEFFER | 87 | 0,87 |
| 22. *Heterotrissocladius grimshawi* EDWARDS | 76 | 0,76 |
| 23. *Stempellinella* BRUNDIN | 62 | 0,62 |
| 24. *Endochironomus tendens* FABRICIUS | 58 | 0,58 |
| 25. *Glyptotendipes* KIEFFER | 48 | 0,48 |
| 26. *Stempellina* (BAUSE) BRUNDIN | 48 | 0,48 |
| 27. *Paratendipes* KIEFFER | 47 | 0,47 |
| 28. *Tanytarsus* v. d. WULP s. str. C | 46 | 0,46 |
| 29. *Cricotopus* (v. d. WULP) EDWARDS | 41 | 0,41 |
| 30. *Corynoneura* (WINN.) EDWARDS | 41 | 0,41 |
| 31. Orth. Genus? *triquetra* CERNOVSKI | 32 | 0,32 |
| 32. *Pagastiella orophila* EDWARDS | 29 | 0,29 |
| 33. *Cryptochironomus* (KIEFFER) LENZ | 23 | 0,23 |
| 34. *Stictochironomus* KIEFFER | 20 | 0,20 |
| 35. *Lenzia* KIEFFER | 19 | 0,19 |
| 36. *Monodiamesa* KIEFFER | 17 | 0,17 |
| 37. *Protanypus* (KIEFFER) EDWARDS | 14 | 0,14 |
| 38. *Endochironomus intextus* WALKER | 12 | 0,12 |
| 39. *Paracladopelma obscura* BRUNDIN | 12 | 0,12 |
| 40. *Parachironomus* LENZ | 11 | 0,11 |
| 41. *Microcricotopus bicolor* ZETTERSTEDT | 11 | 0,11 |
| 42. *Paralauterborniella nigrohalteralis* MALLOCH | 11 | 0,11 |
| 43. *Stenochironomus* KIEFFER | 8 | 0,08 |
| 44. *Einfeldia* KIEFFER | 7 | 0,07 |
| 45. *Paracladopelma* LENZ spp. | 7 | 0,07 |
| 46. *Labrundinia longipalpis* GOETGHEBUER | 4 | 0,04 |
| 47. *Lauterborniella agrayloides* KIEFFER | 3 | 0,03 |
| 48. *Demicryptochironomus* LENZ | 2 | 0,02 |
| 49. *Xenochironomus xenolabis* KIEFFER | 1 | 0,01 |
| Tanypodinae | 1 006 | 10,2 |
| Orthocladiinae | 858 | 8,7 |
| Chironominae | 7 835 | 79,3 |
| Chironomini | 2 688 | 27,2 |
| Tanytarsini | 5 147 | 52,1 |
| undetermined | 174 | 1,7 |
| | 9 873 | 100,0 |

Translator's note: Above columns add up as follows: Taxa 1-49 = 9,696 head capsules (+ the 174 undetermined specimens from below = 9,870). Percentages = 97.19% (+ 1.7% from below = 98.89%). Type columns (bottom): Total No. of specimens = 17,708; total of percentage = 179.2 %.

p.20 cont'd.

The distribution frequency of the Chironomidae throughout the sediment columns, which will be described below, is of greater interest. For each taxon, the number of specimens found per climatic stage will be listed in a Table; in addition, the mean of the relative abundance will be illustrated graphically for the important forms. The distribution of the species is briefly discussed, mainly for the purpose of finding out whether the fossils occur in all sediments with more or less even frequency, or whether their accumulation is higher during certain climatic stages (time-frequency distribution), or in individual cores (place-frequency distribution).

When comparing the absolute values presented in Tables 4-8, it must be kept in mind that more extensive material originating from the younger sediment layers (Subatlantic) was on hand.

There were 32 Chironomidae taxa for which maximal distribution could not be established during any of the climatic stages (Table 4, p. 33): The material was either too scanty to permit an inference of the frequency variations (_Labrundinia longipalpis_, _Stenochironomus_, _Lenzia_), or the specimens were almost evenly distributed throughout the sediment cores (e.g., _Cryptocladopelma_, _Dicrotendipes_, _Polypedilum_); the latter circumstance can hardly be explained with the existence of euryecious organisms which occupied the lake with an equable population ever since the late glacial times, but is due simply to inadequate systematics. Upon identification of the species in question it will probably turn out that several species of the above-mentioned genera existed with varying frequency. The erratic changes in the abundance of the taxon _Tanytarsus_ part. elude interpretation for the same reason because, here also, an unknown number of species hides behind it (Fig. 5, p. 31).

p.21

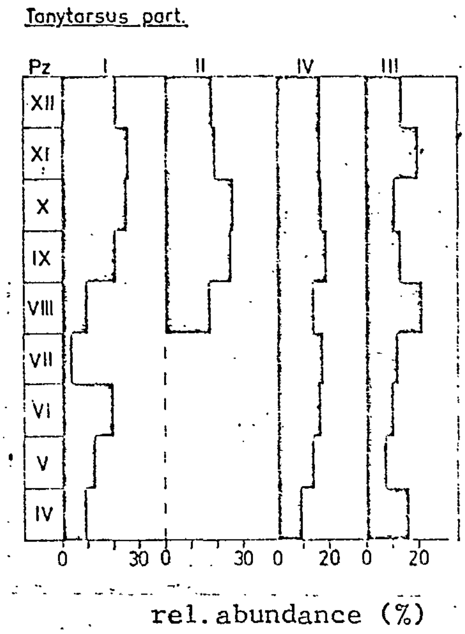

Fig.5

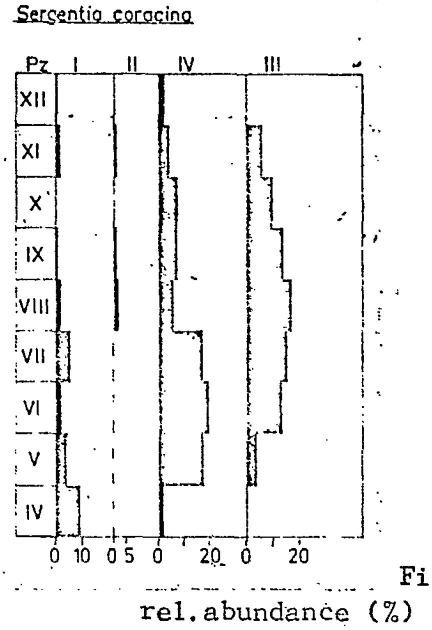

Fig.6

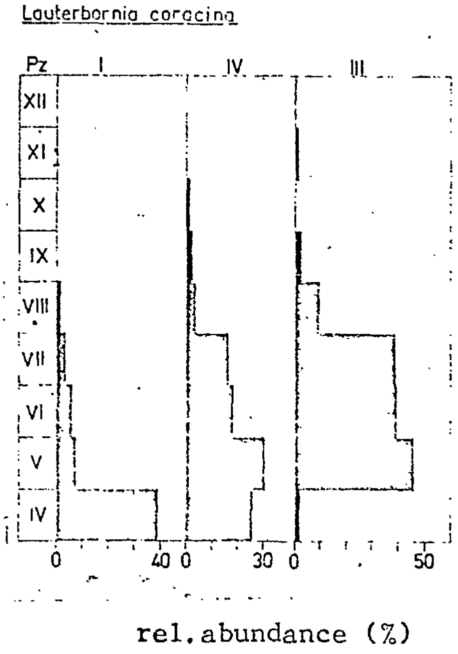

Fig.7

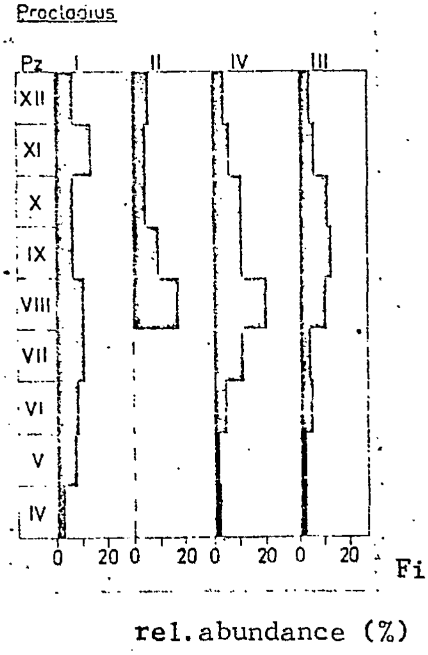

Fig.8

Figs. 5-8: Schöhsee, cores I-IV. Relative abundance (mean) during climatic stages (Pz = pollen zones).

In some cases, certain trends are indicated; for example, the heaviest distribution of the Pentaneurini forms lies for Crocotopus B, Monodiamesa, Orth. triquetra in the older sediments, for Einfeldia in the intermediate horizon, and for Microcricotopus, Stenochironomus, Stempellina in the more recent sediments. p. 20 cont'c

The remaining seventeen taxa as well as Chaoborus can be grouped into the following four distribution types:

The first group is made up by species whose maximum occurs during the early history of the lake, and which later become extinct (Table 5, p. 33).

The presence of Heterotrissocladius grimshawi, Protanypus and Paracladopelma obscura seems to last only from the later Dryas stage p. 22
to the Boreal period. The most frequent of these is Heterotrissocladius which provides 11% of the head capsules from the later Dryas stage of core IV.

Sergentia coracina once played quantitatively an important part in the lake; this is indicated already by its numerous head capsules. The development of this community can be followed directly in Fig. 6 (p. 31).

During the later Dryas stage, the larvae were limited to the littoral/sublittoral zones. In the necrocoenosis of core I, they account for 9% of the Chironomidae, in that of core IV for only 1%. No head capsules were found in sediments from the lower profundal zone (core III).

Toward Preboreal times, Sergentia shifts into deeper waters. It is now most frequent in the upper profundal zone (relative abundance 18%). The frequency decreases visibly in the sublittoral zone (4.6%), and Sergentia appears now in the lower profundal zone (relative abundance 3.6%). p. 23

Table 4: Schöhsee, cores I-IV; Taxa without frequency maximum during any time interval (head capsules per climatic stage). (Total material = extent of total material per climatic stage in relation to Boreal II = 1).

on p.22

| | IV | V | VI | VII | VIII | IX | X | XI | XII | Total | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Labrundinia longip.* | | | | | | | | | 1 | 4 | 1* |
| Pentaneurini | 41 | 19 | 18 | 9 | 11 | 34 | 22 | 56 | 82 | 292 | |
| *Corynoneura* | | | 1 | 3 | 2 | 6 | 3 | 13 | 13 | 41 | |
| *Cricotopus* B | 11 | 9 | 5 | 2 | 2 | 6 | | | 6 | 41 | |
| *Microcricotopus b.* | | | | | 2 | 2 | | 6 | 1 | 11 | |
| *Monodiamesa* | 10 | 3 | | | 1 | 1 | | | 2 | 17 | |
| *Parakiefferiella b.* | 3 | | 4 | 2 | 6 | 21 | 7 | 28 | 16 | 87 | |
| *Psectrocladius* | 11 | 10 | 3 | 1 | 11 | 18 | 15 | 32 | 46 | 147 | |
| Orth. *triquetra* | 3 | 4 | | 4 | 3 | 14 | 1 | | 3 | 32 | |
| *Cryptochironomus* | | 1 | 1 | | 2 | 3 | 3 | 1 | 12 | 23 | |
| *Cryptocladopelma* | 9 | 14 | 17 | 7 | 20 | 51 | 15 | 52 | 42 | 227 | |
| *Demicryptochironomus* | | | | | | 1 | | | 1 | 2 | |
| *Dicrotendipes* | 16 | 8 | 7 | 6 | 7 | 22 | 18 | 72 | 84 | 240 | |
| *Einfeldia* | | | 1 | 1 | 2 | 3 | | | | 7 | |
| *Glyptotendipes* | 4 | 1 | | 1 | | 6 | 3 | 19 | 14 | 48 | |
| *Lauterborniella a.* | | | | | | | 2 | 1 | | 3 | |
| *Lenzia* | | | 1 | | 5 | 4 | 3 | 1 | 5 | 19 | |
| *Pagastiella oroph.* | 1 | | 1 | | 2 | 6 | 5 | 4 | 10 | 29 | |
| *Parachironomus* | 1 | | | | 1 | 3 | 2 | 2 | 2 | 11 | |
| *Paracladopelma* spp. | | | | 1 | 2 | 1 | | 1 | 2 | 7 | |
| *Paralauterborniella* | | | | 1 | 2 | 3 | | 1 | 4 | 11 | |
| *Polypedilum* | 4 | 4 | 5 | 1 | 5 | 25 | 17 | 37 | 59 | 157 | |
| *Pseudochironomus* | | 2 | 1 | 1 | 2 | 1 | 10 | 12 | 63 | 92 | |
| *Stenochironomus* | | | | 1 | 1 | 2 | | 2 | 2 | 8 | |
| *Stictochironomus* | 1 | 2 | | | 1 | 1 | | 4 | 11 | 20 | |
| *Xenochironomus xen.* | | | | | | | | | | 1 | 0* |
| *Paratanytarsus* | 29 | 10 | 11 | 1 | 5 | 42 | 35 | 69 | 55 | 257 | |
| *Stempellina* | | | 2 | | 1 | 16 | 3 | 15 | 11 | 48 | |
| *Stempellinella* | 2 | | 5 | 2 | 3 | 22 | 12 | 10 | 9 | 62 | 65* |
| *Tanytarsus* C | | 3 | 2 | | | 4 | 6 | 14 | 17 | 46 | |
| *Tanytarsus heusd.*-Kreis | 2 | 2 | 5 | 8 | 12 | 28 | 15 | 13 | 31 | 116 | |
| *Tanytarsus* part. | 79 | 55 | 71 | 41 | 65 | 456 | 169 | 349 | 461 | 1746 | |
| Total material: | 4,1 | 1,6 | 1,5 | 1,0 | 1,5 | 7.8 | 2.9 | 6.2 | 8.7 | | |

Table 5: Schöhsee, cores I-IV; Taxa with frequency maximum in the older sediments (head capsules per climatic stage) (Total material= see Table 4 above).

on p.23

| | IV | V | VI | VII | VIII | IX | X | XI | XII | Total |
|---|---|---|---|---|---|---|---|---|---|---|
| *Heterotrissocladius* | 58 | 10 | 8 | | | | | | | 76 |
| *Protanypus* | 2 | 8 | 3 | 1 | | | | | | 14 |
| *Paracladopelma obsc.* | 10 | 2 | | | | | | | | 12 |
| *Sergentia coracina* | 25 | 54 | 64 | 43 | 28 | 83 | 43 | 71 | 16 | 427 |
| *Lauterbornia cor.* | 186 | 146 | 80 | 53 | 14 | 15 | 2 | 1 | | 497 |
| Total material: | 4,1 | 1,6 | 1,5 | 1,0 | 1,5 | 7,8 | 2.9 | 6,2 | 8,7 | |

*) Translator's note: The figures typed to the right of Table 4 are corrections for the total numbers of head capsules, which were misprinted in the last column of the Table.

p.23 cont'd.

The shift into depth continues during Boreal I: The species has now the second-higest frequency among the Chironomidae of the profundal zone, but its optimum is still in the upper horizons of the latter (core IV: 19%). During Boreal II, Sergentia seems to inhabit the entire profundal zone quite evenly (relative abundance in cores III and IV: about 16% each). The frequency decreases steadily in the sublittoral zone of core I. (The high value during Boreal II is doubtful because of the insufficient material.)

Sergentia finally reaches its maximal abundance in the lower profundal zone (core III: 17%). The relative frequency of 17% in the upper profundal zone is reduced to 6%.

The species retains its optimum in the lower profundal zone until the Subatlantic period, but the community becomes visibly smaller, relative abundance decreases steadily: Subboreal I = 14%, Subboreal II = 10%, Subatlantic I = 6%. In the Subatlantic II layer, that is, during the most recent period, Sergentia was no longer detectable in the deep west basin, despite the fact that, here, 900 Chironomidae head capsules were recovered. One specimen from Subatlantic II of core I, and 15 specimens of core IV are proof that a small community still survived in lesser depths.

Lauterbornia coracina also is most frequent during the later Dryas stage in the littoral/sublittoral zones: 39% of the head capsules collected here belong to this species; there were 25% in the sediment of the upper profundal zone. By contrast, only one specimen was found in core III (Fig. 7, p.31).

Decisive changes in the vertical distribution occur during the Preboreal stage. The highest maximal abundance now exists in the lower profundal zone, and the value of about 46% is the highest that was established in the course of these investigations for a Chironomidae species. Nearly every second head capsule of this necrocoenosis counted as Lauterbornia! The frequency rapidly declines in the sublittoral zone: It decreases from 39% to barely 8%. The relative abundance in the upper profundal zone is 30%.

During Boreal I and II, the relative abundance of appr. 40% is p.24 maintained in the deepest strata of the lake; in the upper profundal zone, the relative abundance decreases to 18% and then to 16%.

The climatic transition to the Atlantic stage must have been of extraordinary consequence for Lauterbornia. The community is now drastically decimated: The relative abundance in the lower profundal zone has dwindled to a mere 9%, that in the upper profundal sediment to 3% (in the sublittoral zone 1%). The last trace in core I dates from the Atlantic stage, and in the sediment of core II (the second sublittoral profile) there are no Lauterbornia head capsules at all. A relict community seems to linger on in the profundal zone. The last specimens found in the upper profundal zone were deposited during Subboreal II, the last of the lower profundal zone during Subatlantic I.

The second group (see p.32) consists of three Chironomidae taxa and of Chaoborus. Their maximal abundance occurs during an intermediate period (Table 6).

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Table 6: Schöhsee, cores I-IV; Taxa with a frequency maximum during intermediate period (head capsules per climatic stage). (Total material = extent of total material per climatic stage in relation to Boreal II = 1).

| | IV | V | VI | VII | VIII | IX | X | XI | XII | Total |
|---|---|---|---|---|---|---|---|---|---|---|
| *Procladius* | 19 | 16 | 25 | 30 | 68 | 205 | 81 | 118 | 148 | 710 |
| *Calopsectra* part. | 20 | 24 | 39 | 56 | 61 | 392 | 64 | 138 | 155 | 949 |
| *Corynocera ambigua* | 21 | 3 | 6. | 5 | 16 | 403 | 91 | 74 | | 619 |
| *Chaoborus flavicans* | | 1 | | 1 | 31 | 275 | 158 | 311 | 40 | 817 |
| Total material: | 4,1 | 1,6 | 1,5 | 1,0 | 1,5 | 7,8 | 2,9 | 6,2 | 8,7 | |

As can be seen from Fig. 8 (p. 31), the distribution of Procladius is very uniform. The relative abundance increases and decreases in all four profiles in an almost synchronized fashion. The genus is not frequent during the later Dryas stage (2-3%); the values increase until the Atlantic stage (core IV = 21%!), and are declining again to 4-7% during the following time. In the lower profundal zone, Procladius is less frequent throughout all climatic stages (total mean = 6%) than in the other three sediment cores (8-9%).

During the later Dryas and Preboreal stages, predominantly Pentaneurini head capsules were deposited, Procladius is in the majority during all other stages.

Interpretation of the reported findings is not possible because the Tanypodinae species of the necrocoenosis are unknown to us.

Calopsectra part. ranked second in frequency with 949 specimens (Fig. 9, p. 37). In the necrocoenoses of the sublittoral sediments, relative abundance increases steadily from 3% during the later Dryas stage to 35% during Boreal II. Then, frequency again decreases in the same manner until it reaches once more the value of 3% in the youngest sediment.

During the period from the later Dryas stage until Boreal I, the lower profundal zone is, if at all, inhabited only by Calopsectra p. 26 larvae. Relative abundance stays below 2%. It rises to 8% during Boreal II and the Atlantic stage, and during Subboreal I to almost 20%. The genus is now higher represented in the sediment of the lower profundal zone than in that of the sublittoral zone. Although, during the following stages, frequency values are steadily decreasing, they always remain slightly above those of the sublittoral zone.

on p.2

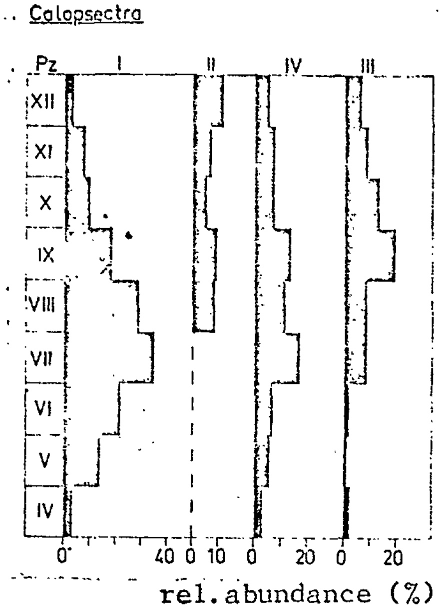


Fig. 9

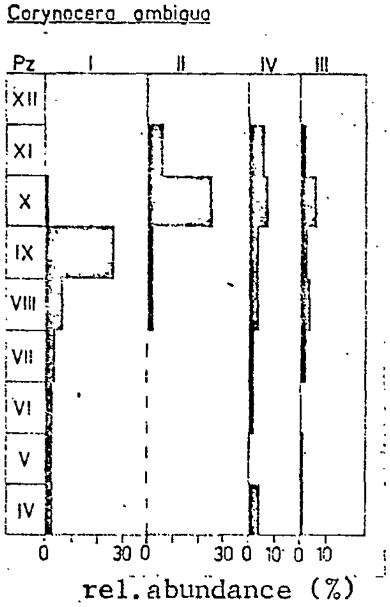


Fig. 10

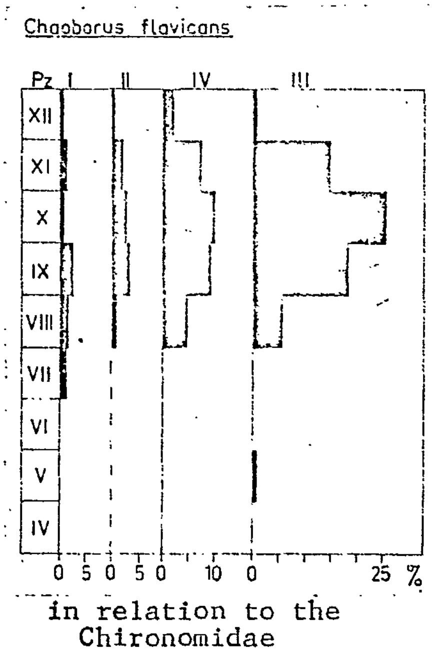


Fig. 12

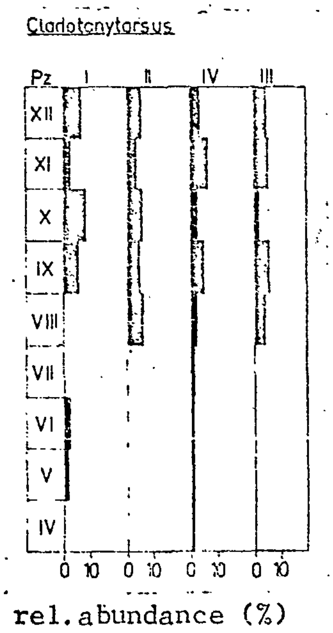


Fig. 13

Figs. 9-10, 12-13: Schöhsee, cores I-IV. Relative abundance (mean) during climatic stages (Pz = pollen zones).

Core IV, which lies with regard to water depth between cores I and II, also has a central position in the frequency of Calopsectra head capsules. The abundance values of the necrocoenoses lie generally between those of the sublittoral and the lower profundal zones.

p. 26 cont'd

The situation in core II differs slightly from the distribution just described. Here, the relative abundance does not decrease during the three last climatic stages, but increases instead so that, in this part of the lake (east bay), Calopsectra seems to be most frequent during Subatlantic II..

Corynocera ambigua (Fig. 10, p. 37) appears as early as in the oldest sediments, but there as well as in the following time it is fairly scarce in the three cores (I, III, and IV). The relative abundance generally amounts to values between 2-4%. The earliest increase in frequency occurs in core I: Here, relative abundance rises to 6% during the Atlantic stage, and then during Subboreal I to 27%. Upon subdividing the latter into two climatic substages, the value arrived at for the early period (1.60-2.70 m) is 34%, for the later period (1.00-1,50 m) = 12.4%, so that the maximal frequency of this species in core I can be fixed to early during Subboreal I. In this connection, one factor should be pointed out which does not become evident from the calculated means: The frequency of Corynocera head capsules in the random samples of core I fluctuates considerably (see Fig. 11, p. 39). Since, here, nearly every sample started out with large amounts of material, these variations can be considered as significant. In the 2.00 m horizon, 126 out of 184 Chironomidae head capsules belong to Corynocera, that is, 68%! In comparison with the considerably lower values of the adjacent samples, such extremely high frequency rates must be taken as evidence of a mass-development of short duration. It is also noteworthy that the number of head capsules diminishes abruptly at the end of Subboreal I: In the Subboreal II sediment, only a single specimen was detected. None was found in Subatlantic sediments.

Coinciding with the time during which this species is extraordinarily frequent in the west-part of the lake, namely during Subboreal I, there develops in the sublittoral zone of the east bay (core II) a Chironomidae necrocoenosis in which Corynocera is represented not even with 2%. It is only when the community of the west-part has practically disappeared that the mean relative abundance increases to 25% during Subboreal II. Here, the species reaches its peak at least a thousand years later.

p. 27

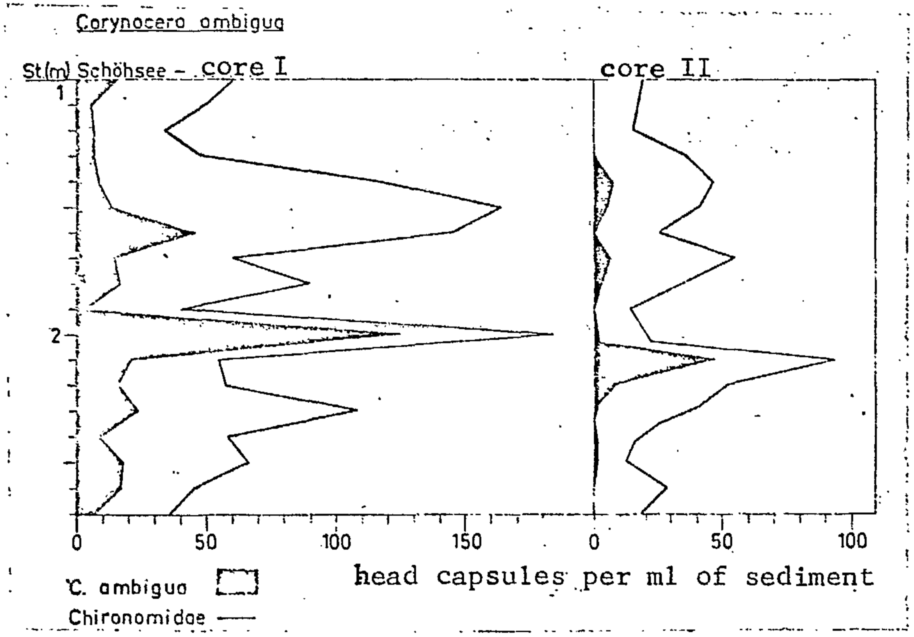


Fig. 11: Schöhsee, core I (1.00-2.70 m), core II (1.00-2.70 m); Corynocera ambigua (number of specimens and of all Chironomidae head capsules in individual samples). [St(m) = depth of sediment expressed in meters.]

Here again, the mean value does not relate the true situation: 47 of the 57 specimens originate from only one sample (2.10 m) in which they represented nearly 50% of all Chironomidae (Fig. 11). In the other samples, on the average only 8% of the head capsules belong to this species. It is therefore not true that Corynocera ambigua was frequent throughout the entire Subboreal II; instead, the species had a mass development at only one point in time which falls in the period at the end of this climatic stage.

In core II, Corynocera has a frequency of 6% during Subatlantic I; no evidence exists for Subatlantic II.

The species is sparsely represented (appr. 2%) in all sediments of cores III and IV; during the Atlantic stage and during Subboreal I, the values are somewhat higher (4-5%) than in the earlier deposits. In both these cores, the species could again not be detected during Subatlantic II.

Chronologically, the distribution of Chaoborus flavicans is also similar to that of the three last-discussed Chironomidae (Fig. 12, p.37; Fig. 20, p.69). While the earliest evidence stems from the Preboreal sediments of core III, regular occurrence of the mandibles begins, however, only with the Atlantic stage. Maximum frequency is reached during Subboreal II (core III: an average of 12 mandibles/ml). During Subatlantic II, frequency greatly diminishes in all sediment cores. Chaoborus is always more frequent in the profundal than in the sublittoral sediments; the highest values are seen in the profile of the lower profundal zone.

The third distribution-type (see p.32) is represented by six Chi- p.28
ronomidae taxa which are most abundant during the most recent climatic stage (Table 7). All of them are littoral forms.

Table 7: Schöhsee, cores I-IV; Taxa with a frequency maximum during the most recent period (head capsules per climatic stage). (Total material = extent of total material per climatic stage in relation to Boreal II = 1.)

| | IV | V | VI | VII | VIII | IX | X | XI | XII | Total | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Cricotopus* A | 13 | 5 | 4 | 2 | 4 | 39 | 30 | 88 | 205 | 391 | 390* |
| *Endochironomus tend.* | | | 2 | | 1 | 2 | 2 | 15 | 36 | 58 | |
| *Endochironomus intext.* | | | | | | | | 5 | 7 | 12 | |
| *Paratendipes* | | | | | 1 | 8 | 8 | 7 | 23 | 47 | |
| *Cladotanytarsus* | 2 | 2 | 4 | 2 | 11 | 123 | 34 | 96 | 129 | 403 | |
| *Thienemanniola* | | | | | | 19 | 22 | 95 | 148 | 284 | |
| Total material: | 4,1 | 1,6 | 1,5 | 1,0 | 1,5 | 7,8 | 2,9 | 6,2 | 8,7 | | |

*) Correction of misprinted total number of Cricotopus A

Cricotopus A was present as early as during the later Dryas stage. The relative abundance (Fig. 18, p.50) remains low in all older sediments; it is never more than 2%. During Subatlantic I (in core IV already during Subboreal II) a distinct increase can be observed. The values increase to 4-5% in all sediment cores, and reach their highest level of 7-8% during the most recent stage. On the whole, distribution is fairly even throughout the sediments of all four cores: The total mean of the relative abundance is 2-3% for all profiles.

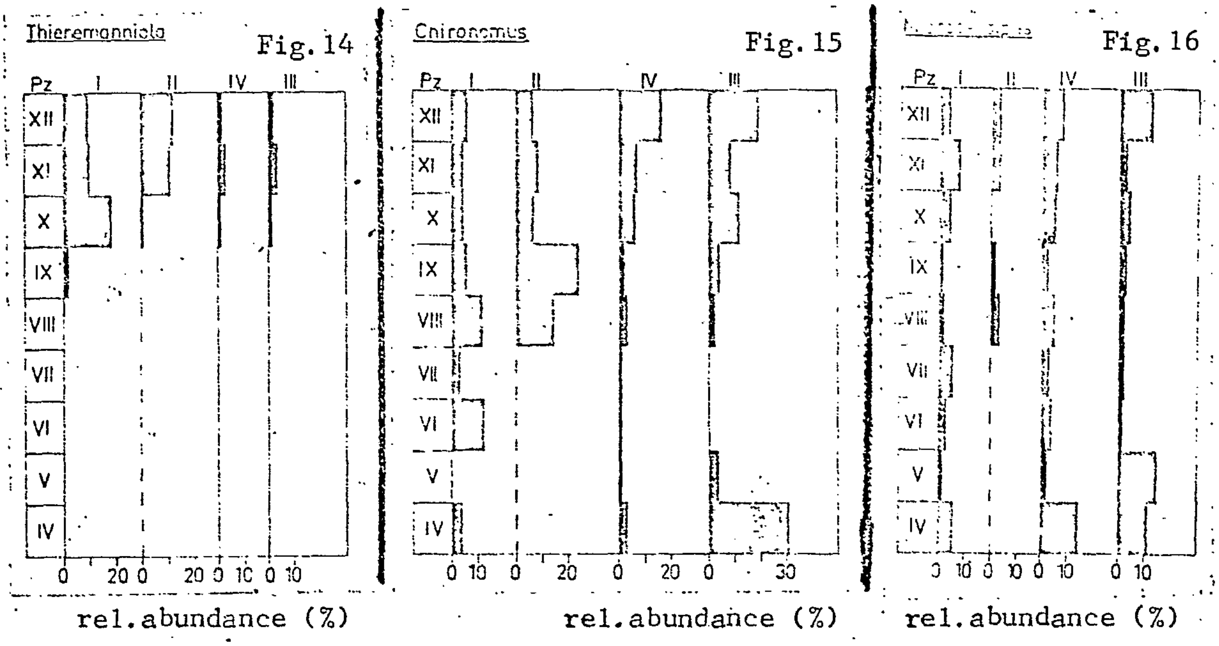
Endochironomus intextus was found only in the Subatlantic sediments, and of the 58 Endochironomus tendens specimens recovered, 51 also originated from this period.

Paratendipes appears first during the Atlantic stage; its frequency increases constantly, up to the youngest sediments.

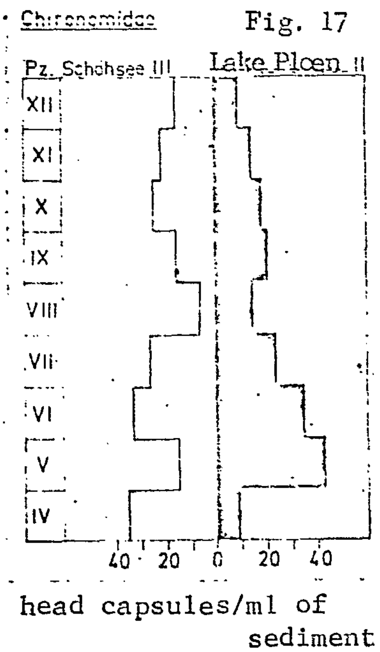
Cladotanytarsus, on the other hand, is present as early as during the later Dryas stage (Fig. 13, p.37). Until Boreal II, this genus is very rare (relative abundance = maximal 2%). During the Atlantic stage (in core I only during Subboreal I), the head capsules become more frequent. Here, the relative abundance is always above 3%, maximal 8%. It is usually somewhat higher in the sublittoral sediments than in those of the profundal zone.

Thienemanniola (Fig. 14, p.42) is a latecomer in the lake, but becomes then very frequent. However, it was no longer detected during recent times. The first specimens appeared during Subboreal I in core I, in the other cores only during Subboreal II. While, in core I, this genus reaches its maximal relative abundance (18%) already during Subboreal II, and becomes again somewhat less frequent during the Subatlantic stages (relative abundance = 10%), there was only one specimen found during Subboreal II of core II, and the highest values came about only during Subatlantic I and II (relative abundance = 12 and 13% respectively).

Both profiles from the profundal zone contained head capsules that were deposited during Subboreal II and both Subatlantic stages. They are not as numerous as in the sublittoral sediments; the relative abundance does not excede 3%.



p. 29



Figs. 14-16: Schöhsee, cores I-IV. Relative abundance (mean) during climatic stages.

Fig. 17: Great Ploen Lake, core II ( = GPS II) Schöhsee, core III. Head capsules per ml of sediment, mean values during climatic stages.

Pz = pollen zones

Finally, the three remaining Chironomidae have a frequency distribution with two maxima: One during the first phase, the other during the last phase of the lake's history (Table 8). It may well-be postulated that each of the two maxima was caused by different species. p.30

Table 8: Schöhsee, cores I-IV; Taxa with two frequency maxima (head capsules per climatic stage). (head caps/clim. stage: see Table 4*)

| | IV | V | VI | VII | VIII | IX | X | XI | XII | Total | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Chironomus* | 63 | 6 | 13 | 3 | 28 | 142 | 56 | 138 | 319 | 758 | 768* |
| *Microtendipes* | 84 | 26 | 14 | 9 | 14 | 40 | 29 | 78 | 175 | 469 | |
| *Tanytarsus* B | 17 | 4 | | | 4 | 9 | 9 | 18 | 57 | 118 | |
| head caps/clim. stage: | 4,1 | 1,6 | 1,5 | 1,0 | 1,5 | 7,8 | 2,9 | 6,2 | 8,7 | | |

During the later Dryas stage, the dominant Chironomidae genus in the lower profundal zone of the lake is Chironomus (Fig. 5, p.31). Here, the genus has a relative abundance of 30% which is never again equaled. It is surprising that Chironomus contributes only 3% of the head capsules in that part of the lake where depth is less by only a few meters (core IV). In the sediment of core I, relative frequency is 4%.

The Chironomus population is drastically reduced when the Preboreal approaches: A mere 4% of the head capsules still belong to this genus. A decrease is observed also in lesser depths (core IV).

During Boreal I and II, Chironomus disappears almost completely from the deep strata (relative abundance = 1%); the larvae become more frequent in the sublittoral zone: 13% during Boreal I, 4% during Boreal II. Because of the limited material, both these values are subject to a large probable error, but the figures mentioned show nevertheless that, at this time, Chironomus was fairly frequent in shallower zones (represented by core I), but rarely present in deep strata.

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*) Translator's note: Translated as printed; however, in Table 4 as well as in Tables 5-7, it always reads "Total material" and is explained as such. Therefore, reference to Table 4 would be confusing since the reader would not recognize the equivalent, except for the values in this row which are identical in all Tables. -- 768 = correction of misprinted total number

This type of vertical distribution is maintained also during the Atlantic stage. Now, also the values from core II are available which further strengthen the concept of vertical distribution: Here, Chironomus constitutes 15% of the necrocoenosis, in core I it is 12%; in both the profundal cores, the values reach only 2-3%.

While no substantial changes take place during Subboreal I, the Chironomus larvae are in the process if migrating into depth during Subboreal II: Relative abundance increases in the profundal sediments (core III = 12%, core IV = 6%), and, simultaneously, decreases in the sublittoral sediments (core I = 4%, core II = 7%). The genus is now most frequent in the lower profundal zone. During Subatlantic II, Chironomus has established itself as a distinctly profundal community: The relative abundance of the head capsules is 17% (core IV) to 20% (core III) in the profundal zone, and 6% (cores I and II) in the sublittoral zone. p.31

The most important Chironomus species in the Baltic lakes are Chironomus anthracinus, and Chironomus plumosus. Comparisons between recent larvae of both these species from different lakes resulted in the observation of distinguishing characteristics on labium and mandibles. In accordance with this principle, the subfossorial material was divided into "anthracinus" and "plumosus" head capsules. Since, in older sediments, we are not necessarily dealing exclusively with these two species, their designations are enclosed by quotation marks.

This differentiation of Chironomus head capsules revealed several new details: The maximum during the later Dryas stage differs in its composition from all other, more recent, necrocoenoses, because here, the "plumosus" forms are in the majority whereas, during the other stages, "anthracinus" is always most frequent.

It can be shown, furthermore, that the eurybathic migration described above as beginning during Subboreal II, is instigated by "*anthracinus*" larvae. As can be seen from Table 9, initially, the latter are more frequent in sublittoral than in profundal sediments; starting with Boreal II, exactly the opposite is true.

*Table 9*: Percentage of "*anthracinus*" head capsules in *Chironomus* necrocoenoses.

| Pollen zones: | IV-IX | X-XII |
|---|---|---|
| Core I | 93.7% | 64.2% |
| Core II | 72.1% | 61.2% |
| Core IV | 64.3% | 75.3% |
| Core III | 55.5% | 75.1% |

This hypothesis is supported also by the recent vertical distribution: *Chironomus plumosus* was not found below 19 m in the Schöhsee, whereas *anthracinus* advances all the way into the lower profundal zone.

The chronological distribution of *Microtendipes* is similar to that of *Chironomus* (Fig. 16, p. 42). During the later Dryas stage, this genus provides 12% of the Chironomidae in core III, and 14% in core IV. While, in the former, relative abundance still experiences a slight increase during Preboreal times (15%), it decreases to 1.6% in core IV. Since the corresponding values in the sublittoral sediment (core I) are low during both [illegible] climatic stages (pollen zone IV = 5.5%, pollen zone V = 1.5%), it seems likely, nevertheless, that a *Microtendipes* community existed which populated the entire profundal zone during the later Dryas stage, but was limited to the lower profundal zone during the Preboreal stage.

Beginning with Boreal I, the head capsules become quite scarce in all cores. Relative abundances usually amount to 2-4%, and are particularly low in core III.

Increasing frequency can be observed throughout Subboreal II (except in core II). While the increase is initially minimal, relative abundance then increases in core III during Subatlantic II to 12.3%, and thus reaches again the level that prevailed during the later Dryas and Preboreal stages. Even core IV shows here a maximum (relative abundance = 8%). Less frequent (relative abundance = 4%) are the head capsules in the sublittoral sediments.

Both maxima of the genus Microtendipes are due to the vigorous development of profundal communities.

The two maxima in the distribution of Tanytarsus B were to be expected alone on account of the gap in the findings during the Boreal period. This prediction was borne out by the fact that relative abundance is at a peak during the later Dryas stage on the one hand, and during the Subatlantic period on the other.

Before general conclusions are drwan on the basis of the hitherto illustrated distribution types, or any attempt is made to view the results in relation to the history of the lake, the outcome of a similar investigation of a sediment core from the neighbouring Great Ploen Lake shall be reported and compared with the conditions encoutered in the Schöhsee.

## C. Comparative study on Great Ploen Lake

Great Ploen Lake is the prototype of a eutrophic Baltic lake and, with a surface area of appr. 30 sq. km, the largest inland water in Holstein. Its maximal depth is 60.5 m, the average depth is 16 m (WEGEMANN 1922 : 24). It differs from the Schöhsee not only by its larger and deeper basin, but also -- for example -- by the higher calcium content of its water (OHLE

1934), and by the character of its sediment. In contrast to the Schöhsee, true gyttja is deposited in Great Ploen Lake (UNGEMACH 1960 : 171). Common to both lakes if the fact that, in the hypolimnion, oxygen depletion sets in during summer stagnation (OHLE 1953 : 153-154).

The sediment core to be discussed here was bored from the deep portion of the lake near the city of Ploen, which is greatly affected by domestic sewage (UNGEMACH 1960 : 169). It appears that macroscopic bottom fauna does not exist below 20 m; random sampling with a pedonic hoist produced neither Chironomidae, nor Chaoborus, nor Tubificidae (cf. ALSTERBERG 1925 : 334).

The sediment core had a total length of 15.10 m; water depth at the bore location was 41.20 m.

The pollen-analytical work was performed by AVERDIECK (not yet published). The demarcation of the pollen zones is based on the same criteria as those employed by SAAD (1960 : 18-25) for the dating of the Schöhsee sediments. At the time when the present paper was prepared, the investigation by AVERDIECK was not quite completed, so that the demarcations p.33 of the pollen zones indicated here are not necessarily to be considered as final. Doubtful was still the border between zones XI/XII. So as to bypass this problem in the present work, a provisional "zone" XIa was placed between zones XI and XII. It must be emphasized, however, that XIa does not represent an actual pollen zone but merely serves as a temporary solution for the purpose of synchronizing the results of this Chironomidae investigation with pollen-analytically defined reference points. "Zone" XIa begins with the rational increase of pine trees and lasts until the pine maximum and beech-tree decline. The actual XI/XII border lies somewhere in the vicinity of that "zone". The oldest sediments date, just as in the Schöhsee, back to the later Dryas stage.

It is not intended to reconstruct here the history of the Chironomidae fauna of Great Ploen Lake; this is easier to accomplish in the case of the much smaller Schöhsee on the basis of the four sediment cores. The investigation of this one core was undertaken for the purpose of relating to it the findings from the Schöhsee. The risk of applying the answers found in one lake to other lakes as well is all too apparent.

Special consideration must be given to core II of the Schöhsee when comparing the results, because it stems from the greatest depth of water. Furthermore, it must also be kept in mind that depth at this site is 15 m less than at the deep of Great Ploen Lake near the city of Ploen.

From the core of Great Ploen Lake (GPS II) a total of 1,540 Chironomidae head capsules and 6 Chaoborus mandibles were recovered. Fossil density seems to be grouped around an average value. A concentration of high or low values, the formation of distinct maxima and minima as seen in the Schöhsee-cores (Fig. 3, p. 22), cannot be readily recognized here. However, the profile of the average fossil density per climatic period shows many similarities with core III (Fig. 17, p. 42). The only discrepancy concerns the later Dryas and Preboreal stages: While in core III the highest mean (35 specimens/ml) was found in the later Dryas sediments, it is precisely then that a minimum (9 specimens/ml) is observed in GPS II which has the maximum (43 specimens/ml) only during the Preboreal period. From then on afterwards, the values are steadily declining. The regularity is disturbed only by the particularly low value that occurs during the Atlantic stage. Precisely the same tendency was seen also in core II where, in addition, the number of head capsules was low also during Subboreal I. It is noteworthy that the total mean of head capsules per ml of sediment amounts to 21 specimens/ml in both cores.

No additional taxa were discovered in GPS II, but some of the Chironomidae listed for the Schöhsee are missing. They are those which are scarce even there, and could not really be expected to be among the considerably less extensive material of GPS II:

*Labrundinia longipalpis* p.34
*Protanypus*
*Demicryptochironomus*
*Endochironomus intextus*
*Lauterborniella agrayloides*
*Paracladopelma* spp.
*Stenochironomus*
*Xenochironomus xenolabis*

Of the 41 taxa found in either lake, large numbers were too rare to strengthen the individual distribution profiles described before. Some differ slightly from the Schöhsee-profile:

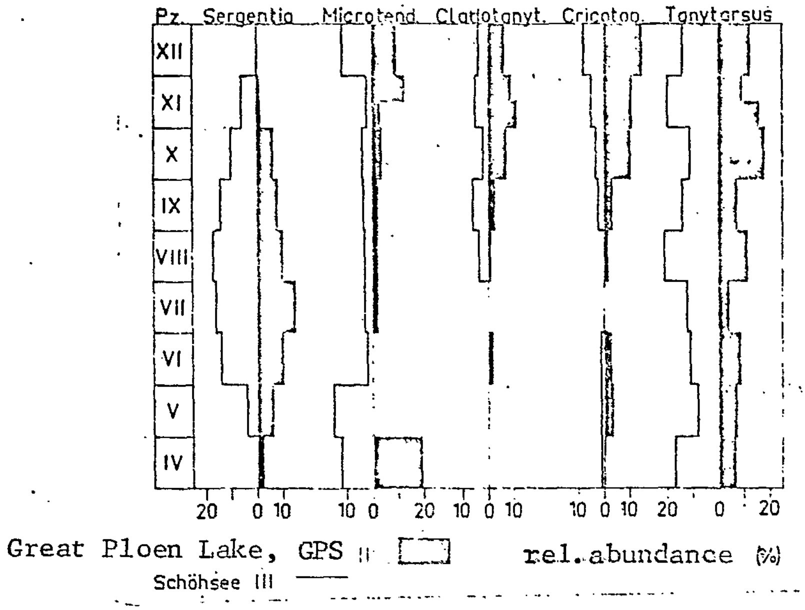
Heterotrissocladius grimshawi is more frequent in GPS II than in core III; relative abundance is about 8% during the later Dryas and Preboreal stages and thus closer related to core IV (11 and 2% respectively). An important difference lies in the fact that, in GPS II, the species is represented by scattered individuals until Subatlantic I, whereas, in all Schöhsee-cores, it could be traced only as far as Boreal I. Maximal frequency coincides in both lakes during the later Dryas stage and the Preboreal period.

In addition to three Paracladopelma obscura specimens from the later Dryas stage, one was found also during the Atlantic stage. In the Schöhsee, this species was observed only until the Preboreal.

Paratendipes does not appear in the Schöhsee before the Atlantic stage. In GPS II, proof of its presence comes already from the Preboreal. However, the peak occurs here also during the Atlantic stage and the periods thereafter: 29 of the 31 head capsules come from those times. p.35

Fig. 18: Great Ploen Lake, core GPS II; Schöhsee, core III; Sergentia coracina, Microtendipes, Cricotopus A, Cladotanytarsus, Tanytarsus part.; Relative abundance (mean) during climatic stages. (Pz = pollen zones)

on p.34



Because of the greater significance of values obtained of frequent species, these are more likely to confirm or disprove the Schöhsee-results. The mean relative abundances of the eight most important taxa are illustrated in Figs.18 and 19 (p.51) in comparison with the values of core III. Six of these are well in agreement (Fig.18). This is particularly obvious in the case of Sergentia coracina, but also very distinct in the profiles of Microtendipes, Cricotopus, and Cladotanytarsus. The values of Tanytarsus part. show irregular fluctuations in both cores without revealing any tendency.

p.35
cont'

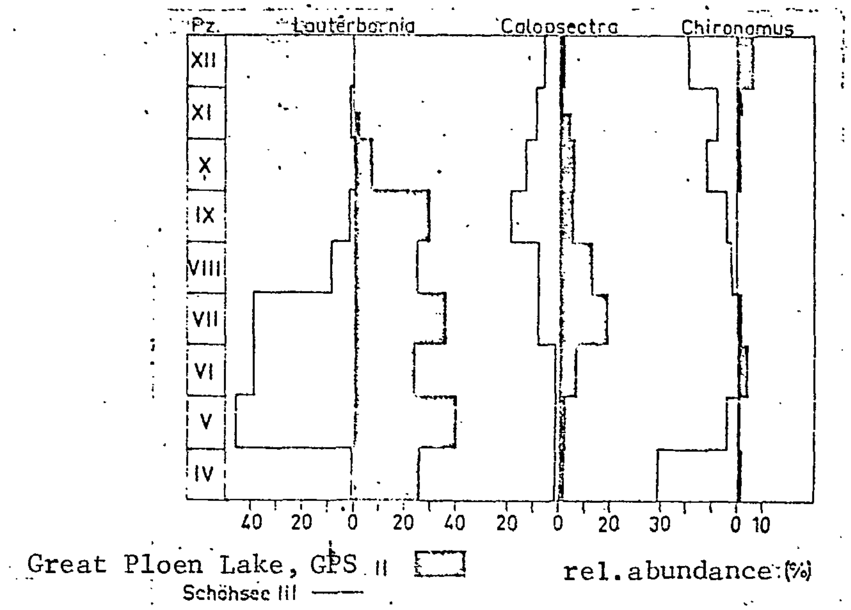
Chironomus (Fig. 19, p.51) differs insofar as the maximum observed in core III during the Dryas stage fails to appear in GPS II. Also, in the latter, this species is anyway far less frequent (barely 2% of all the head capsules) than in core III (11%). Apart from that, there is a maximum during Subatlantic II in both profiles.

Lauterbornia coracina (Fig. 19) played an even greater role in Great Ploen Lake than in the Schöhsee: From the later Dryas stage until Subboreal I, the species represents 25-40% of all head capsules. This abundance decreases only during Subboreal II, and the last findings date from Subatlantic I. In core III, only a limited number of specimens were found during the later Dryas stage (by contrast, relative abundance in core IV is 25%). After the relative frequency has climbed to about 40%, it decreases drastically as early as during the Atlantic stage, that is, 5,000 years before it does so in Great Ploen Lake.

p.36

Fig. 19: Great Ploen Lake, core GPS II; Schöhsee, core III; Chironomus, Lauterbornia coracina, Calopsectra part. Relative abundance (mean) during climatic stages. (Pz = pollen zones)

on p.3



Calopsectra has basically the same distribution, but in core GPS II, the maximum appears sooner.

p.36 cont'd

On the whole, it can be stated that the values for the Chironomidae are throughout well in agreement. None of the taxa ~~has~~ in either lake shows a fundamentally different distribution: Differences exist only insofar as some taxa appear sooner in core GPS II than in the Schöhsee (*Paratendipes*), while others turned up in younger segments (*Heterotrissocladius grimshawi*, *Paracladopelma obscura*). On the other hand, surprising congruencies were observed: Synchronous increases and decreases in the relative frequency of *Sergentia coracina*. It is noteworthy also that *Microtendipes* and *Tanytarsus* B have each two maxima in either lake. When the sediment core from Great Ploen Lake was set up as control investigation to ensure the essential accuracy of the Schöhsee-results, it turned out that the chronological distribution of the Chironomidae in the Schöhsee is not an accidental observation, since it was fully confirmed by this collation.

An important contrast between the two lakes manifests itself in the case of *Chaoborus flavicans*: In GPS II, only six mandibles were counted (all from the Subatlantic stage), but there were 394 in core III. If the number of paired mandibles is expressed as a percentage of the Chironomidae head capsules, this results in a value of less than 2% for core GPS II during the Subatlantic stage — the only segment in which *Chaoborus* was encountered. In core III, the relation amounts to 18% during Subboreal I, 25% during Subboreal II, and 15% during Subatlantic I. Great Ploen Lake apparently never had a strong *Chaoborus* community, and this is true even today.

### D. Subfossorial hypopygia

It is the first time that not only the head capsules of larvae were recovered, but that subfossorial hypopygia of the imagoes were also found in lake sediments. In most cases, only few abdominal sections still adhered to them, but frequently there were also parts of pupal skin (section VIII) and swimmerets attached (Fig. 25*). This means that these were animals whose pupae did not ascend to the surface of the water. The process of breaking the pupal case was disturbed, and they remained with the mature imagoes in the sediment.

It can be seen from Table 10 that, in relation to the head capsules, the number of hypopygia is very low. But even these few furnish important information in two respects:

Table 10: Schöhsee, Great Ploen Lake; list of subfossorial hypopygia (number of specimens between parentheses) p. 3

| Pollen zone | Schöhsee core I | Schöhsee core IV | Great Ploen Lake core GPS II |
|---|---|---|---|
| XII | *Thienemanniola* (1) | *Chironomus* (1) | *Psectrocladius* (1)<br>*Cladotanytarsus* (1) |
| XI | | | *Parakiefferiella* (1)<br>*Cladotanytarsus* (2)<br>*Parat. penicill.* (1) |
| X | *Corynocera a.* (1) | | *Sergent. coracina* (1) |
| IX | | *Cricotopus* (1) | *Lauterb. coracina* (4)<br>*Calops* cf. *lugens* (1)<br>*Tanyt. signatus* (1) |
| VIII | | | *Lauterb. coracina* (1)<br>*Micropsectra* (1) |
| VII | | *Cricotopus* (1)<br>*Tanyt. niger* (1) | *Lauterb. coracina* (1)<br>*Tanytarsus* (1) |
| VI | *Tanyt. niger* (1) | | *Lauterb. coracina* (3)<br>*Tanyt. niger* (1) |
| V | | *Lauterb. corac.* (1) | |
| IV | *Chironomus* (1) | | |

First, the great number of Lauterbornia coracina specimens support the supposition that the later described head capsules belong indeed to this particular species.

Second, three species were established which could not be identified with the help of the larval material: Tanytarsus niger, Tanytarsus signatus, and Paratanytarsus penicillatus. Tanytarsus niger corresponds completely to the form found in Lake Stechlin (Mecklenburg Lake Plateau, East Germany) and described by MOTHES (1966a : 260).

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*) Translator's note: There are only 22 Figures in this text; none of these is an actual illustration of an insect, or its larval or pupal stages.

## VIII. Existence-ecological aspects of taxa distribution

The variations in the Chironomidae fauna during the postglacial period which were described here are closely related to the development of the biotope, that is, to the history of the lake. In the following chapter, an attempt will be made to discuss these relations individually.

The most important ecological conditions which affect the pedonic fauna of an inland water are: temperature, oxygen and food supply. In what way did these factors fluctuate, and how can the faunal succession be synchronized with such fluctuations?

### A. Temperature

The postglacial temperature cycles in Central Europe are well known. Three stages can be distinguished during the period of time which is of interest here:

1. A climate which is colder than at the present time (mean July temperature 7-8°C below the current average) = Later Dryas stage. p.38

2. A climate which is warmer than at the present time (Atlantic stage: mean July temperature 2-3°C above the current average [SCHWARZBACH 1961 179]): Boreal to Subboreal I.

3. The recent climate prevailing since Subboreal II.

It is evident that temperature changes affect primarily the littoral zone of a lake, whereas low temperatures prevail constantly throughout the profundal zone. During the month of August ~~in~~ the temperature of the Schöhsee-water at a depth of 25 m is 7.4°C, in Lake Semningsjön (Jämtland, Sweden), located at the borderline between birch-region and arctic region, 8°C were measured at a depth of 24 m during the same month (BRUNDIN 1949 : 257). In addition, the following data are available: The mean temperature for the month of July (1851-1930) in Kiel (Schleswig-Holstein, Germany) is 16.2°C (Klimakunde des Deutschen Reiches [= Climatography of Germany] 1939 : 17). The average of 10°C indicated for the region of Lake Semningsjön (Atlas över Sverige [Atlas of Sweden] chart 25) corresponds approximately to the temperature which supposedly prevailed in the province of Holstein (Germany) during the later Dryas stage. This example illustrates how little influence such temperature differences have on the conditions in the profundal zone.

If, here, the questions are to be answered whether any relationship becomes manifest between the temperature changes and the variations in the abundance of the Chironomidae, and if so: what kind of relationship, only species from the littoral and sublittoral zones can be taken into account.

In arguing this point, numerous papers can be cited in which the Chironomidae are characterized according to their temperature requirements, and are classified either as stenothermal, cold-limited forms, or as eurythermal organisms. The results of those investigations were arrived at by establishing the temperature range within which a given species lives, taking into account its entire geographical range. The present work on subfossorial Chironomidae makes it possible to observe directly the behavior of Chironomidae species in the event of temperature changes.

As was discussed, some Chironomidae (Heterotrissocladius grimshawi, Protanypus, Paracladopelma obscura) can be found only in the oldest sediment layers, and temperatures at that time were very much below the present standards, although they rose considerably as early as during the Preboreal. It is tempting, therefore, to relate the disappearance of species to the rising temperatures, all the more so as, according to BRUNDIN

(1949), these were more or less cold-limited, stenothermal species (this applies to all species of the genus *Protanypus*). However, considering that they are eurythermal organisms which occupy the littoral zone in subarctic lakes, and the profundal zone in the oligotrophic lakes of Central and South Sweden (BRUNDIN 1949), it then follows that temperature cannot be the factor that drives the species out of the Schöhsee, be- p. 39 cause it could have retreated into the constantly cold profundal zone. In fact, it could be shown that *Heterotrissocladius grimshawi* managed to survive in the depth of Great Ploen Lake even until Subboreal times.

The other two species that were counted as distribution-type A accomplished the shift into depth on a large scale: *Sergentia coracina* and *Lauerbornia coracina*. During the later Dryas stage, their abundance maximum occurs in the littoral/sublittoral zones, and, beginning with the Preboreal stage, in the profundal zone. Their present range corresponds to this distribution pattern: In arctic and subarctic inland waters, both Chironomidae species dwell in the littoral zone, while in Central European lakes they restrict themselves to the profundal zone (BRUNDIN 1949 : 773-774, 786). By contrast, REISS (1968b : 271-272) found *Lauterbornia* predominantly in the upper sublittoral zone (depth 4-7 m) of Lake Constance, and only occasionally also in depth of up to 25 m. *Sergentia* is, here also, decidedly concentrated in the profundal zone (REISS 1968b : 268). *Lauterbornia* inhabits primarily the depth of Schaalsee, Madüsee, and the oligotrophic crater lakes of the Eifel region (Germany) (THIENEMANN 1915; 1918 : 21, 27). By analysing the necrocoenoses it could be shown that both types of vertical distribution, the arctic/subarctic as well as the North and Central European type, occur consecutively in the history of the Schöhsee.

It can be suspected that the first abundance maximum of taxa that belong to the fourth distribution type (p.43) is instigated by other species than those which caused the second peak. It can also be assumed that they are cold-oriented stenothermal organisms. However, without knowledge of the participating species, this amounts to mere speculation, even if *Chironomus* species (*Chironomus hyperboreus*, *Chironomus lugubris*), and a *Microtendipes* species (*M. brevitarsis*) are known from arctic and subarctic inland waters (BRUNDIN 1949 : 737; THIENEMANN 1954 : 568). In the case of *Tanytarsus* B it is doubtful anyway which species belong to the type of larva under discussion.

It could be expected that, during the postglacial cycle of warmth -- irrespective of the shift by cold-oriented stenothermal species -- the eurythermal or warmth-limited, stenothermal Chironomidae are at their optimum.

*Calopsectra* part. exhibits maximal frequency in the sublittoral sediment (core I) during Boreal II and the Atlantic stage. However, this has hardly any direct bearing on temperature conditions since, later, the taxon shifts into the profundal zone. Furthermore, the species considered here (*Calopsectra lugens*, *Calopsectra tripunctata*) are by no means partial to warmth (BRUNDIN 1949 : 804-805; REISS 1968b : 270-271).

*Corynocera ambigua* is also extraordinarily abundant throughout the sublittoral zone (core I) during Subboreal I. This fact cannot be directly connected with prevailing high temperatures: The species has existed in the lake already since the later Subarctic times, and during Subboreal II -- that is, after the climate started to deteriorate -- it shows once more a short-termed mass-development. BRUNDIN (1949 : 184) characterizes the larva p.40

as an eurytherm, the pupa as a cold-limited stenotherm, and MOTHES (1968 : 92-93) established that, in Lake Nehmitz (Mecklenburg, Germany), the species outlasts the summer in its egg-state, which, in MOTHES' opinion, indicates "a certain cold-oriented stenothermia."

In Lake Sompiojärvi (Finnish Lapland) the first imagoes start leaving the pupal case when part of the surface is still covered with ice, the height of eclosion time is when the water reaches a temperature of about 7°C (HIRVENOJA 1960 : 158). Interestingly enough, HIRVENOJA established in the same lake a marked mass-development of Corynocera (up to 12,000 specimens/sq.m); the very high distribution in the Schöhsee-sediments during the Subboreal period suggests a similar phenomenon.

The other species of the second distribution-type (p.35) have their optimum in the profundal zone; they are not affected by temperature changes.

Therefore, maximal abundance is not in evidence for warmth-orientated species during the postglacial warm period.

It is equally unfounded to hold the climatic deterioration, which then followed, directly responsible for the changes among the Chironomidae fauna: Neither do warmth-limited, stenothermal forms decrease — perhaps with the exception of Labrundinia longipalpis (see p.92) — nor do cold-oriented, stenothermal species gain new grounds. The taxa of the third and fourth distribution types that could come under consideration here do not account for any distinctly cold-limited forms. This does not necessarily mean that these temperature fluctuations exert merely a minor influence, but could be due to the fact that only few members of the Chironomidae family are classified down to their species, so that abundance maxima of some species are suppressed, and also to the fact that the littoral forms are covered very inadequately with the method employed here.

## B. Oxygen

The postglacial temperature fluctuations had a direct effect only on the littoral zone. Considerable fluctuations in the oxygen content of the water are, however, to be expected only in the hypolimnion. Therefore, changes in the profundal Chironomidae fauna may probably have to be interpreted as a consequence of fluctuations in the hypolimnetic oxygen level. In this case, it must of course be stipulated that the requirements of the species in question concerning the oxygen content of the milieu are known; with respect to the Chironomidae to be discussed here, they are in fact known. There exist not only a number of reports on profundal Chironomidae in various lakes which discuss also the hypolimnetic oxygen conditions (THIENEMANN 1915, 1920, 1922; LUNDBECK 1926, 1936; BRUNDIN 1949), but experimental investigations on the respiratory physiology of several species have also been reported (e.g., HARNISCH 1937, 1943; BERG et al. 1962). It is therefore justified, if – for example – a polyoxybiontic specimen disappears and, simultaneously, an euryoxybiontic species settles in, to relate this occurrence to at least a temporary decrease in oxygen content. p. 41

During the later Dryas stage, the Chironomidae fauna of the lower profundal zone differs decisively from that of the upper profundal zone. At least two Chironomus species are dominant in deep strata; Lauterbornia, Sergentia, and Heterotrissocladius are limited to the littoral and upper profundal zones. Chironomus larvae generally count as euryoxybiontic, and their predominance in a biotope is indicative of an oxygen-poor milieu (THIENEMANN 1915, 1918; LUNDBECK 1926, 1936; LENZ 1925; BRUNDIN 1949); Lauterbornia coracina, Sergentia coracina, and Heterotrissocladius grimshawi are – to varying degrees – polyoxybiontic organisms. On the basis of the vertical distribution established in these findings, there is every reason to believe that temporary oxygen deficiency existed during the Subarctic stage in the deepest strata of the Schöhsee.

Under similar climatic conditions, oxygen depletion and $H_2S$-production can actually occur in inland waters, namely when they are icebound for too long, and the water volume is too small to store enough oxygen for the duration of that period (ANDERSEN 1946 : 21, 30, 34; cf. THIENEMANN 1922). However, ANDERSEN's data relate to shallowwaters of the High Arctic (Ella Island, Greenland) in which Chironomus hyperboreus was found, but hardly in greater depth than 1 m. But BRUNDIN (1942) observed that Chironomus larvae are dominant also in the profundal zones of several lakes in Jämtland (Sweden) which are located in the range of a climate about similar to that prevailing in North Germany during the later Dryas stage. In one of these waters, only 0.77 mg $O_2$/liter was found immediately above the floor, at a total water depth of 13 m. Unfortunately, in the paper cited, only the $O_2$-values during July are listed; nothing is stated about oxygen conditions underneath an ice cover.

The oxygen content in deep, subarctic lakes is, according to BRUNDIN (1949 : 580), at a constant high so that the difference between the profundal Chironomidae fauna in the Schöhsee and that of Great Ploen Lake during the later Dryas stage may, perhaps, be due to the heterogeneous morphology of these two lake basins.

* During the Preboreal and Boreal stages, the profundal Chironomidae fauna of the Schöhsee and of Great Ploen Lake consists mainly of Lauterbornia and Sergentia larvae, the former being distinctly in the majority. Upon

* In the warm postglacial period that followed, the cause of any oxygen deficiency is perhapsattributable to a pronounced summer stagnation rather than an ice cover of long duration.

summarizing the data furnished by diverse authors on the oxygen demand of both these species, it turns out that Sergentia has a greater tolerance for low $O_2$-concentrations than Lauterbornia. THIENEMANN (1915 : 26) p.42 found Lauterbornia in the oligotrophic crater lakes of the Eifel region only if $O_2$-values (August-October) were above 6.4 mg/liter; in the two North German "Lauterbornia-lakes", Madüsee and Schaalsee, the oxygen content in the pedonic strata was 4.7-5.4 mg/liter.

Sergentia coracina is found in the profundal zone of lakes in the Warta district* (Lake Schrimm, Lake Gorzyn, Great Tucsen Lake, Puls Lake) with $O_2$-values of 2.5-4.6 mg/liter. Sergentia avoids the deepest parts of Lake Altgörzig, where the hypolimnetic $O_2$-concentration is even less (1.3 mg/liter) (THIENEMANN 1928 : 22-31; cf. STAHL 1966). These data are well in agreement with the observations of WÜLKERS. This author reports that Sergentia larvae leave the pedonic mud of the Titisee when $O_2$-concentration reaches a critical level of about 2 mg/liter, and withdraw into the pelagial zone (WÜLKER 1961a : 963-964).

If these data are taken at face value and applied to the appropriate phase of development in the lake, it then follows that, at the end of summer stagnation, the depth of either lake must have had an approximate supply of at least 5 mg $O_2$/liter.

Thus, the sudden decrease in numbers of the stenoxybiontic species Lauterbornia coracina during the Atlantic stage must be taken as a sign of deteriorating oxygen conditions. This hypothesis is further supported by the fact that, for the first time, Chaoborus flavicans appears in greater amounts in the lower profundal zone. These larvae inhabit mainly the profundal zone of oxygen-deficient lakes (THIENEMANN 1915, 1922; LUNDBECK 1926, 1936; BRUNDIN 1949; ALSTERBERG 1925).

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*) Translator's note: "Warthegebiet" = Warta district; formerly in Germany, since 1945 part of Poland.

By contrast, favorable oxygen conditions prevail in Great Ploen Lake until Subboreal I; until then, Lauterbornia coracina is the most frequent Chironomidae species in the profundal zone. Since Great Ploen Lake has the greater mean depth, the suspected differences in the hypolimnetic oxygen levels of the two lakes correspond to the different morphology of both lake basins (cf. LUNDBECK 1936 : 332).

During Subboreal I, the Sergentia population begins to decrease, whereas Chaoborus markedly increases; furthermore, greater numbers of Calopsectra larvae are now added which appear to fit well into this, with regard to oxygen content not particularly favorable, milieu. THIENEMANN (1929 : 106) says of the Calopsectra species (these are generally identical with the species which REISS [1968b : 203-204] grouped into the newly classified genus Calopsectra): "All of them are true mud dwellers with a great capacity for adaptability to the existing $O_2$-content." Calopsectra larvae are found even today in the profundal zone of the Schöhsee (cf. p. 6) which speaks indeed for their modest demands on the oxygen content. All indications point to a continued lowering of oxygen standards in the profundal zone at a time when a considerable portion of the pedonic fauna in Great Ploen Lake still consists of Lauterbornia coracina.

The next developmental stage is characterized by the fact that Chironomus larvae which, until then, occupied the sublittoral zone, invade the profundal zone and thus supplement the assemblage of euryoxybiontic organisms (THIENEMANN 1915, 1922; LUNDBECK 1926, 1936; HARNISCH 1937, 1943; BERG & JÓNASSON 1965; BRUNDIN 1949). Then, during Subatlantic II, species of the genus Chironomus are the most frequent inhabitants of the profundal zone in the Schöhsee. p.43

Beginning with Subboreal II, a process similar to that occurring in the Schöhsee takes place also in Great Ploen Lake: The abundance of Lauterbornia decreases suddenly, and the frequency of Sergentia also continues to lessen. The last specimens of either genus were recovered from sediments accumulated during Subatlantic I. This process is accompanied by an enormous increase in the speed of sedimentation.

However, the composition of the necrocoenoses gives no indication that the evacuated terrain is conquered by euryoxybiontic species. Although the Chironomus portion of the head capsules shows a slight increase, this portion amounts to barely 7% of the total yield from the latest sediments. Calopsectra is quantitatively of no importance. The frequency of Chaoborus is minimal. Instead, a large number of head capsules from littoral Chironomidae appears, and of others which are definitely not native to the profundal zone: Cricotopus, Cladotanytarsus, Microtendipes. Specimens of the genus Microtendipes belong in all probability mostly to the species Microtendipes pedellus which has been observed in the littoral and sublittoral zones (HUMPHRIES 1938 : 547; LENZ 1942 : 45). The larvae of Tanytarsus part. must also be considered as littoral elements. HUMPHRIES (1938 : 549) observed that, in Great Ploen Lake, only Tanytarsus samboni is present also in greather depths. The profundal Chironomidae Chironomus and Calopsectra account, together, not even for 10% of the head capsules. An increasing frequency of littorigenic elements in the profundal necrocoenoses can be observed also in the later Schöhsee-sediments; this phenomenon will be dealt with in detail later (p.76).

It is the general impression that, in the course of the history of the Schöhsee, the hypolimnetic oxygen standard gradually declined.

This process becomes apparent during the Atlantic stage when *Lauterbornia* experiences its decimation. Later, *Sergentia* also disappears. Instead, *Chaoborus flavicans*, *Calopsectra*, and *Chironomus* one by one invade the profundal zone. It is possible, however, that the first victims of this development were even those Chironomidae which inhabited the lake only at the very beginning, and which we have combined into the first distribution-type (*Heterotrissocladius grimshawi*, *Protanypus*, *Paracladopelma obscura*). As eurybathic organisms, they could have easily escaped into the profundal zone during the postglacial period of warmth; it seems that, even then, oxygen conditions were already too unfavorable to allow such a shift. It is interesting that *Heterotrissocladius grimshawi* survives considerably longer in the depth of Great Ploen Lake where, because of the greater hypolimnion, the milieu was perhaps more favorable. In this p.44
lake, the $O_2$-conditions of the profundal zone do not change before Subboreal II.

## C. Food

The food factor is very complex and difficult to appraise. Its importance for the development of the Chironomidae fauna can only be implied. It is by no means evident from the chemical data (e.g., the content of organic matter) supplied by SAAD (1966 : Figs. 23-27) for the Schöhsee-sediments, which types of gyttja are especially poor, or particularly well-suited, as food for certain Chironomidae larvae. The particular food requirements of the individual species are practically unknown. It is known, though, that some species are found only on very nutritive substrates, while others find enough food also in mineral sediments (LUNDBECK 1936; BRUNDIN 1949; REISS 1968b).

A mineral sediment was deposited during the later Dryas stage. Apart from the unidentified Chironomus species, it was inhabited, among others, by Heterotrissocladius grimshawi, Protanypus, Paracladopelma obscura, Cricotopus alpicolus which, then, disappear almost simultaneously with the transition to more nutritive gyttja deposits. These species are more or less polyoxybiontic and cold-limited stenothermal organisms which are therefore, if for no other reason, found mostly in an oligotrophic milieu that is at the same time characterized by nutrient-poor sediments. It is therefore difficult to appraise which factor decisively determines the presence of the species. The sediment plays no role whatsoever as a source of food for the predacious forms Protanypus (PAGAST 1947 : 563) and Paracladopelma (HARNISCH 1923; PAGAST 1947 : 568; THIENEMANN 1954 : 59-60).

The fact that Lauterbornia and Sergentia shift during the postglacial warm period more and more toward depth may have something to do with the circumstance that profundal sediments were then more eutrophic than during the early history of the lake.

REISS (1968b : 271) postulates that food is the regulating factor of the Calopsectra tripunctata population in Lake Constance.

JONASSON & KRISTIANSEN (1967) have shown that the growth of Chironomus anthracinus larvae depends heavily upon food supply.

LUNDBECK (1936 : 295-298) placed great importance on the food factor in the development of a profundal population. BRUNDIN (1949 : 655) comments on the problem as follows: "While it is the oxygen factor that excludes the species which are characteristic of oligotrophic lakes from the eutrophic lakes, it is the food factor that keeps the characteristic species of eutrophic lakes from developing more strongly in oligotrophic lakes." After all, an $O_2$-deficient milieu as such is hardly an attraction for Chironomus larvae to dwell in it. It can be assumed that, in all the observed shifts into deeper strata (Lauterbornia, Sergentia, Calopsectra, Chironomus), increased concentration of nutrients in the profundal sediments is also of importance. p.45

D. Remarks concerning Chaoborus flavicans

The factors which decide the absence or presence of Chaoborus flavicans larvae in the profundal zone of a lake have been investigated by many authors (THIENEMANN 1915, 1922; VALLE 1927 : 74-80; ALSTERBERG 1925 : 321; LUNDBECK 1926, 1936; BERG 1937 : 23-24). In summary, the results illustrate a rather ambiguous distribution to the various lakes: While Chaoborus favors waters with a low oxygen content in the pedonic strata, it may well be missing there, but may be present also in lakes with higher hypolimnetic $O_2$-content. ALSTERBERG (loc. cit.) points out that the larvae may be absent from lakes with gyttja deposits, but were always present where the bottom is covered with ooze*; VALLE also reports (loc. cit.) that they are particularly abundant in humous lakes. BRUNDIN (1949 : 410) summarizes: Within the investigated territory (South Sweden), Chaoborus larvae find "optimal conditions only in the polyhumous, natural lakes, and in the Växjö lakes which show marked artificial eutrophication." More simplified, one could say: The abundance of Chaoborus larvae has a positive correlation with the humus content, and a negative correlation with the oxygen content of the water.

Of the lakes investigated here, only Schöhsee has Chaoborus flavicans in its profundal zone. LUNDBECK (1926) did not find the species in Great Ploen Lake. In this respect, it is of importance that the dis-

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*) Translator's note: In the original, the term "Dy", which is of Swedish origin, is used here to denote deposits rich in disintegrated organic material.

tance between both lakes is only a few hundred meters, that both lakes have $O_2$-depletion in the hypolimnion during summer stagnation, and that neither of them is a humous lake.

In the Schöhsee, larger amounts of Chaoborus appeared for the first time when the Lauterbornia population collapsed. This is well in agreement with the above-cited opinions. However, in Great Ploen Lake, the profundal pedon is at that time still characterized by a strong Lauterbornia community and, as long as it survives, thus indicating a high oxygen content in deep strata, Chaoborus cannot be expected to appear.

We have already learned that even later when oxygen conditions deteriorate, Chaoborus mandibles are not nearly as frequent in these necrocoenoses as in the Schöhsee. Therefore, realizing that the difference between the pedonic faunas in both lakes has already existed for thousands of years, one has to look for the causes in the past.

With regard to the hypolimnetic $O_2$-level, it has been established that the development in Great Ploen Lake was similar to that of Schöhsee, but considerably delayed.

As mentioned before, the humus factor plays an important role in the distribution of Chaoborus. Although the calcium content of the Schöhsee is lower than that of Great Ploen Lake, the former is still not a humous lake and does not deposit ooze, but a mineral sediment. However, in this connection, it is of great interest that UNGEMACH (1960 : 183-186) found an older, autochthonous gyttja below the recent sediment, which "with 3.8% Ca in the dry substance is particularly poor in lime" (Table 11, p.74). "In this respect it shows similarities to the transitional type between the lime-deficient gyttjas and the humous sediments such as were often observed p.46

in lakes with limited influx of lime and of nutrients, e.g., in the Bültsee and Ihlsee." (UNGEMACH loc.cit.)

So as to examine the fossorial sediments for their humus content, all random samples of Schöhsee-core III and some samples of GPS II were analyzed for their humic acid content (see p. 9).

As a first result of this investigation it was established that, for long stretches, Schöhsee-sediments are considerably more enriched with humic acids than the GPS II sediments. In the latter, the values are at a constant low (unfortunately, the uppermost layer — a few meters — could not be analyzed; here also, the sediment samples were rich in lime, as was shown upon admixture of HCl). The humic acid values found in core III are "inversely proportional" to the lime content reported by SAAD (1966 : 84-86).

Upon comparing the extinction values with the distribution of Chaoborus mandibles as illustrated graphically in Fig. 20 (p.69), it becomes obvious that a correlation exists between them. This fact offers two explanations:

1. Chaoborus larvae were more frequent when the humus content was higher. This is in agreement with previous observations regarding the distribution of this species.

2. The mandibles were better preserved when humic acid concentration was higher because the pH-value was correspondingly low and bacterial activity was thus curbed. This problem ought to be clarified by laboratory tests.

The second hypothesis would explain why so few mandibles have been recovered from recent sediments despite the fact that the Chaoborus population was very large at the time of LUNDBECK's investigation, and that it is so even now. Investigation of the profundal top-sediments of Lake Esrom (Zealand, Denmark) revealed a similar situation: The abundance of Chaoborus larvae in the profundal zone amounts to over 1,000 specimens/sq.m (BERG 1937), but in the sediment — in contrast to the numerous head capsules of Chironomus anthracinus — mandibles were found only in isolated instances.

However, it would also be conceivable that the underrepresentation of this species in the necrocoenoses is merely due to the fact that the larvae are not restricted to the sediment and regularly wander into the limnetic strata (BERG 1937 : 50-89). Thereby, a great number of exoskeletons are discarded in open waters, float to the surface, and are blown away by the wind. It is the opinion of DEEVEY (1942 : 261) that:

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p.47

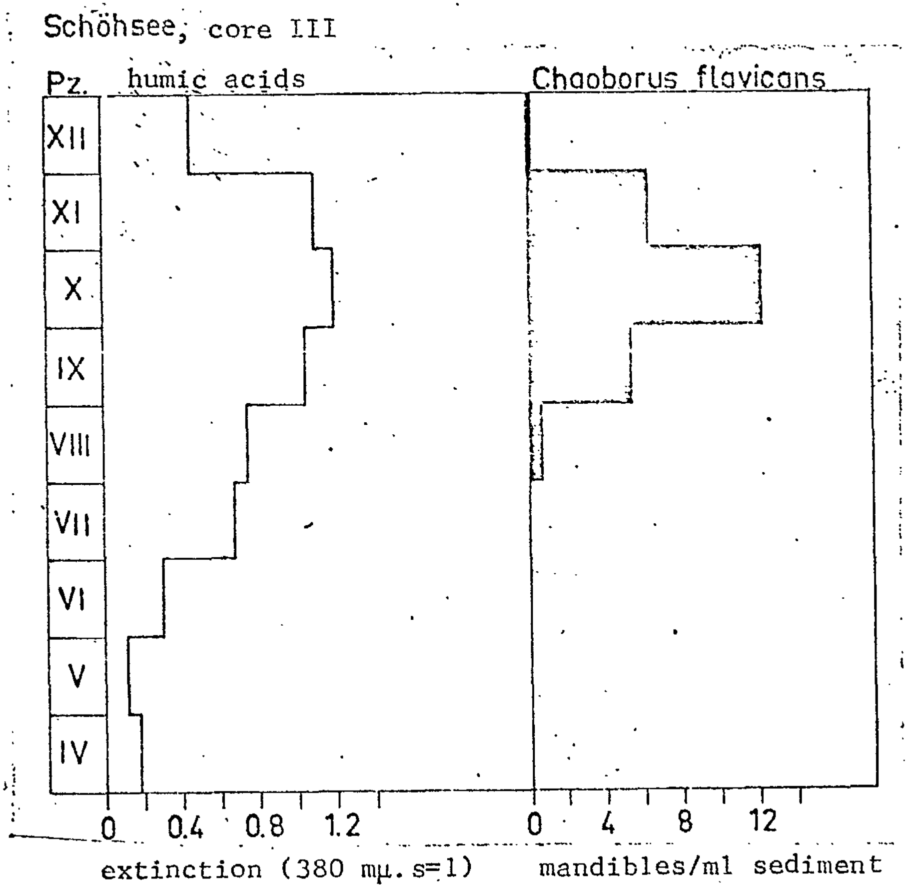

Fig. 20: Schöhsee, core III; Chaoborus flavicans (number of mandibles (mean) per ml of sediment during climatic stages). Humic acid (average extinction values during climatic periods). Pz ≙ pollen zones.

"The numbers (of Chaoborus-remains in the sediment) 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." If for this reason most mandibles do not show up in the inspected necrocoenoses, the abundance of larvae during the Subboreal stage and Subatlantic I must have been all the greater in the Schöhsee. Therefore, the recent community would have to be considered as relict from those periods.

Whether the greater abundance of Chaoborus mandibles in Subboreal and Subatlantic I is due to better conditions for survival in the humus-rich milieu, or whether the larvae were generally more numerous at that time, cannot be conclusively determined here. The second version has a greater probability in view of the fact that the mandibles, found in the gyttjas of Great Ploen Lake and Lake Esrom, are well preserved and show no sign of bacterial destruction. p.48

## IX. Ecology of the pedonic fauna during the past forty years

During the twenties, the lakes around Ploen were for the first time the object of intensive investigations on a large scale. With regard to their pedonic faunas, a number of publications exist which document the conditions then prevailing: The extensive treatise on the world of pedonic animals in North German lakes by LUNDBECK (1926), the writings of THIENEMANN (1920, 1922) in which he relates his findings from the crater lakes in the Eifel region to the lakes in Holstein and Mecklenburg, as well as the investigation conducted by ALSTERBERG (1925).

The development of the past four decades can therefore easily be reconstructed, and this method is of course much more direct than the evaluation of necrocoenoses. Moreover, information is now available on additional pedonic organisms and on oxygen conditions. Comparison with those investigations offers great advantages also because microfossil density in the Schöhsee is very low due to the allochthonous attenuation of the sediment so that the available material is very limited, and because the last developmental phase in Great Ploen Lake remained rather obscure due to the predominantly littoral elements in the profundal sediment. Here, the limitations of the method employed become evident.

Schöhsee

In Fig. 21 (p.72), the distribution frequency of Chironomidae larvae, Chaoborus larvae, and Tubificidae as calculated by LUNDBECK (1926 : 444) is compared with the values arrived at during the present investigations (see pp. 4-8).

In discussing the differences, only substantial discrepancies can be taken into consideration; minor deviations may have been introduced by the method.

In 1924, there were still 550 specimens/sq.m of Chironomus anthracinus found at a depth of 20-24 m, and 350 specimens/sq.m where water depth was more than 24 m. The Chironomus abundances observed by THIENEMANN (1922 : 616) in several samples on June 30th, 1920, correspond to these values: 16 m = 360 specimens/sq.m, 20 m = 1,000 specimens/sq.m., 30 m = 40 specimens/sq.m. However, during recent years, only 10 specimens/sq.m (west basin) and 20 specimens/sq.m (east basin) were found at 20 to 30 m depth. Chironomus plumosus was completely absent below 20 m. This indicates an extensive withdrawal of both these Chironomus species from the profundal zone. It is also interesting that the ratio between the number of Chironomus larvae and that of all other Chironomidae larvae in the profundal zone underwent fundamental changes: While the ratio between Chironomus p.49 and other Choronomidae was 4.5 : 1 in LUNDBECK's investigation, it is now 1:4 in the east basin and 1:3 in the west basin.

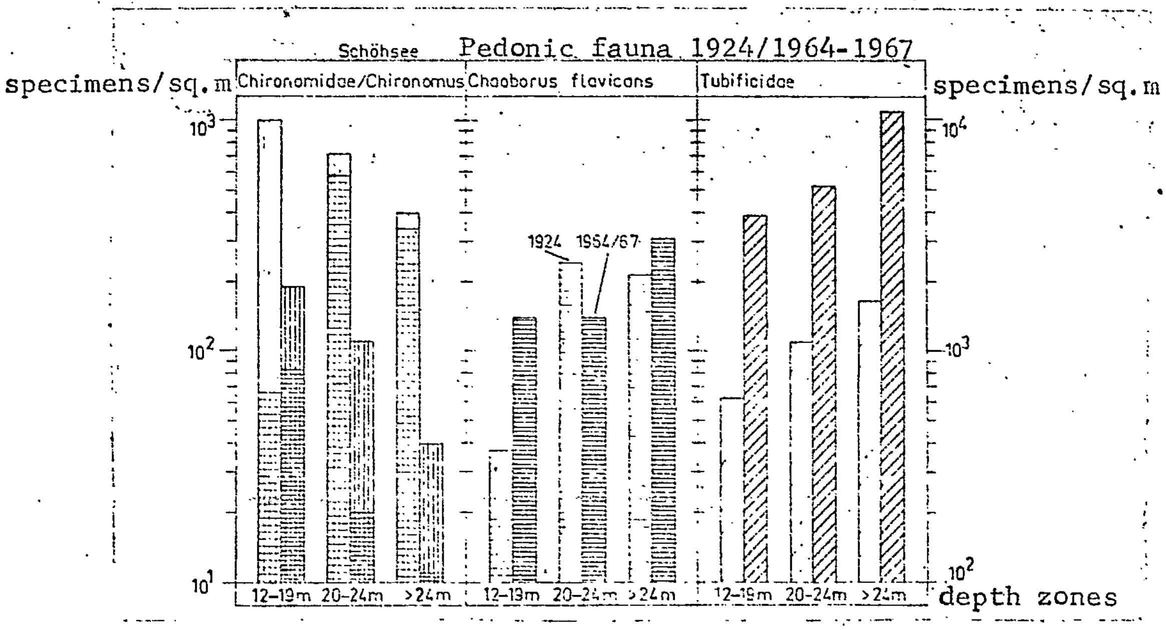

Fig. 21: Schöhsee; abundance of organisms in the profundal pedon in the year 1924 (after LUNDBECK 1926) and during 1964-1967.

In the depth zone of 12-20 m, the frequency distribution of both Chironomus species remained about the same.

The frequency distribution of the other Chironomidae species shows a slight decrease in the lower profundal zone, but the decline is spectacular in the 12-19 m depth zone. LUNDBECK reports values of 580 and 1,200 specimens/sq.m; calculations from our dredge-samples (see pp. 6-7) resulted in a mere 110 specimens/sq.m.

With regard to Chaoborus flavicans, the situation of 1924 was very similar to present conditions. The 1924 decrease in the abundances

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Translator's note: The term "benthos" used in Fig.21 and sometimes in the text of the original, has been replaced by "pedon" according to Allee & Schmidt, Ecol.Animal Geography, University of Chicago Press, p.390: "Communities dependent on the bottom...belong to the benthos in oceans and to the pedon (pedonic) in lakes."

established for the 12-20 m depth zone must not be overrated since the Chaoborus larvae are subject to seasonal vertical migration and may have still been concentrated in the pedonic stratum during April.

While a decrease was observed in the Chironomus community of the lower profundal zone, a considerable increase becomes obvious in the frequency of Tubificidae. LUNDBECK's calculations amounted to 1,700 specimens/sq.m for the lower portion of the 20-30 m depth zone, and to 1,100 specimens/sq.m for the upper portion. The samples of recent years reveal an abundance of 5,300 specimens/sq.m in the east basin, and of 10,800 specimens/sq.m in the west basin. Also in the 12-19 m depth zone, Tubificidae are now much more frequent (3,900 specimens/sq.m) than at the time of LUNDBECK's investigation (325 and 950 specimens/sq.m).

In summary, it can be stated that the profundal Chironomidae population, especially that of Chironomus has markedly declined over those forty years, whereas the abundance of Tubificidae has extraordinarily increased; the situation remained stable only in the case of Chaoborus flavicans. p. 50

While searching for the causes of these changes, a close look must be taken, first of all, at the oxygen conditions. Comparison of the measurements conducted by THIENEMANN (1922 : 626) in the summer months of 1917 to 1920 with those established for 1965 and 1967 reveals indeed an enormous deterioration of the hypolimnetic oxygen levels. In addition to one zero-value, THIENEMANN reports $O_2$-concentrations of 1.5 to 4.1 mg $O_2$/liter in depths of 24 to 29 m, whereas now, the hypolimnion is completely depleted of oxygen below 15 m during the same months.

Furthermore, construction work on the embankment of the north shore of the lake was started only in the thirties. Before that time, no clayish mineral sediment existed in the profundal zone; instead, the "old autochthonous gyttja" was observed by UNGEMACH (1960 : 183-186) which is now beneath this allochthonous sediment. These gyttja deposits differ in many respects from the recent top sediment, as evidenced by the compilation of some of the values from the paper by UNGEMACH (Table 11).

Table 11: Schöhsee; chemical components of recent top sediments (depth zone 27 m), and of the gyttja deposited underneath (after UNGEMACH 1960); d.s. = dry substance

| depth of mud (cm) | organic subst. (% d.s.) | humic acids (% d.s.) | organic carbon (% d.s.) | chlorophyll (% d.s.) | Fe (% d.s.) | Ca (% d.s.) |
|---|---|---|---|---|---|---|
| 0-4 | 9.8 | 0.74 | 3.4 | 0.0036 | 4.7 | 5.3 |
| 4-8 | 14.0 | 1.50 | 5.2 | 0.0064 | 4.7 | 3.8 |

If the top sediment is relatively calcium-deficient, this applies all the more to the gyttja directly underneath which is, thus, leading over to humous sediments (UNGEMACH 1960 : 183-186). Since the organic components constitute the larger part in the composition of the sediment, it can be said that it had greater nutritive value; this factor is of importance to the mud-consuming pedonic organisms.

Thus, the profundal milieu has changed in two respects: On the one hand, it is more oxygen-deficient during summer stagnation and, on the other hand, it has also become poorer in nutrients. This constellation — oxygen and food shortage — which does not normally exist in the profundal zone of the lakes, has instigated the extensive displacement of the Chironomus larvae from the lower profundal zone. What remains is a peculiar Chironomidae population; the individual species can only be considered as relicts: None of them lives here under optimal conditions, all of them have an extremely low population density. Polypedulum nubeculosum, the most frequent of these species, has in the west basin an abundance of p.51 only about 15 specimens/sq.m. By contrast, the Tubificidae were extraordinarily promoted by this development, The larvae of Chaoborus flavicans, according to their population density, remained indifferent.

Great Ploen Lake

Core GPS II was bored from the deep portion of the lake near the city of Ploen; the depth at the bore location was appr. 41 m. Only a few dredge samples suffice to show that a pedonic fauna no longer exists at that depth level. Even in far lesser depth (up to 20 m), hardly any pedonic organisms are observed.

ALSTERBERG (1925 : 334) already reports that a pedonic fauna in the "hypolimnetic region" is nonexistent because of the $O_2$-deficiency due to overabundant food influx. It also becomes evident from LUNDBECK's Table (1926 : 446-447) that, at depths over 30 m, hardly any pedonic organisms were found.

The hypolimnetic oxygen conditions were, at that time, not all that unfavorable: THIENEMANN (1922 : 625) analyzed samples from the deep portion of the lake near the city (depth 40 m) and found $O_2$- concentrations of more than 3 mg $O_2$/liter (except for one value which showed 1.8 mg $O_2$/liter) during the months of July to September of the years 1916 to 1921. OHLE (1953 : 153-154) emphasizes that oxygen contents were steadily decreasing since 1926. In 1951, only very minimal amounts ($<$ 1 mg $O_2$/liter) were present above 14 m, and no oxygen at all after 23 m of depth. Besides this, $H_2S$ accumulated in the hypolimnion.

The absence of a pedonic fauna from the deep portion of the lake near the city explained by such adverse conditions in the milieu; however, this does not explain the fact that, despite sufficient $O_2$-stores and despite the substrate being rich in nutrients, neither Chironomidae nor Tubificidae have been found in the lower profundal zone ever since the early twenties. Understandable is, however, the peculiar composition of the necrocoenosis in this sediment. It is certain that, here, head capsules of littoral Chironomidae predominate which were washed in from other strata.

Taking into consideration that, despite the favorable conditions still prevailing at the time of the investigations by THIENEMANN, LUNDBECK, and ALSTERBERG, the pedonic fauna was already wiped out at a depth of 40 m, it could perhaps be postulated also that this condition existed already throughout the entire Subatlantic period. This hypothesis would explain the unusual necrocoenoses. Then, by far, most of the head capsules would be "allochthonous", that is, the larvae would have been carried after eclosion from far away here to the deepest spot of the basin. This kind of assemblage of head capsules in the sediment does not represent a necrocoenosis, but a thanatocoenosis in the sense used by WASMUND (1929).

It is probable that, initially, a great number of Chironomidae larvae still lived in the profundal zone, but due to the enormous increase of the sedimentation-rate the "autochthonous" fossil density in the sediment was markedly reduced. However, since littorigenic elements contribute extensively to sedimentation, and since considerable amounts of head capsules of obligate stenobathic organisms are transported into the profundal zone, total fossil density remains high. p.52

It is not surprising that it was hardly possible to trace the latest development of the pedonic fauna on the basis of necrocoenoses. There are two reasons: 1. Since the frequency of Chironomidae larvae is limited, the number of head capsules deposited in the sediment is, as such, also small, and 2. the necrocoenoses have been "diluted" by allochthenous additions. This does not only lead to the limited fossil density (in core III = 1 specimen/ml), but it also causes the littoral elements — which were anyway present in limited numbers in all profundal necrocoenoses — to become prominent; therefore, the composition of the necrocoenosis no longer provides direct information about past population dynamics at the sample site.

These circumstances were much more evident in the younger sediments of Great Ploen Lake than in those of the Schöhsee. But even in the sediments of Schöhsee-core III do Cricotopus head capsules represent 8% of the Chironomidae-remains. In addition, there are many other stenobathic organisms; their total number very drastically lowers the relative abundance of the true profundal organisms, e.g., that of Chironomus. The share of 19% which Chironomus head capsules represent in the necrocoenosis (core III, Subatlantic II), surely does not correspond to the actual participation of Chironomus larvae in the profundal biocoenosis of the past; it must have been considerably more extensive. Therefore, the results obtained by evaluating the necrocoenoses must be viewed very critically if the above-mentioned adverse conditions exist.

Whenever a strong Chironomidae population existed at the sediment sample site, the "autochthonous" head capsules are bound to outnumber the "allochthonous" specimens. This has been manifest not only in the older sediments in which the vertical distribution of the species was clearly visible and where the vertical migration of some species was demonstrable, but was obvious also from investigations of profundal top sediments from lakes with known pedonic faunas. In Lake Esrom, this necrocoenosis consisted almost exclusively of head capsules from *Chironomus anthracinus*; in addition, there were a few mandibles of *Chaoborus flavicans*. The uniformity of this necrocoenosis is possible because a strong *anthracinus* community exists, and because the lake's basin is very wide and the slope is relatively gradual. Therefore, head capsules from the littoral zone are very seldomly carried into the middle of the lake. By contrast, none of the Schöhsee bore-locations — nor that of core GPS II — is far away from the shoreline, and the edge has in all instances, particularly p.53 near bore-location IV, a rather steep slope so that littoral detritus is easily washed down.

## X. Lake types according to pedonic fauna

Within the scope of this work we shall dispense with discussing the bottom-faunal lake types. One must not be tempted to present, offhand, the profundal Chironomidae successions as a sequence of lake types. Neither shall the history of type-limnology nor the extensive literature on this topic be dealt with here; in this respect, reference is made to the comprehensive writings by BRUNDIN (1949 : 616-669; 1956 : 186-191) and THIENEMANN (1954 : 385-518).

Basing classification in the customary manner on the most abundant Chironomidae of the lower profundal zone — in our case the species representing the necrocoenoses in core III — the stages of development are as follows:

1. Later Dryas stage: *Chironomus*
2. Preboreal-Boreal: *Lauterbornia*/*Sergentia*
3. Atlantic stage: *Tanytarsus*/*Sergentia*; *Chaoborus*
4. Subboreal I: *Calopsectra*/*Sergentia*/*Tanytarsus*; *Chaoborus*
5. Subboreal II — Subatlantic I: *Calopsectra*/*Tanytarsus*/*Chironomus*/*Sergentia*; *Chaoborus*
6. Subatlantic II: *Chironomus*/*Tanytarsus*; *Chaoborus*
7. Subatlantic II, recent: *Polypedilum nubeculosum*, *Chironomus anthracinus*, *Calopsectra*, *Tanytarsus*, *Chaoborus*

Apart from the "Chironomus-lake" of Dryas times, and disregarding the present stage, this order represents a lake-type succession as it was called for by LUNDBECK (1936 : 295-298) on the basis of comparison with recent lake characteristics: During the first developmental phase, the oxygen-rich, nutrient-deficient profundal zone is inhabited by Orthocladiinae larvae. However, as soon as the sediment becomes richer in nutrients due to increased production in the lake, the "Tanytarsus community" from the littoral zone settles in. Further enhancement of production renders the milieu still more favorable with respect to nutritive conditions, but because of the accumulation of organic substances, oxygen depletion has already begun. The Tanytarsus community is driven away and Sergentia takes its place. The ecological conditions further develop in the same direction: Enrichment with nutrients and, consequently, $O_2$-depletion, so that Sergentia is forced into the sublittoral zone, while Chironomus anthracinus now pushes from there into the profundal zone. The subsequent development is such that, after a phase of Chironomus plumosus predominance, Chironomidae larvae can no longer exist in the $O_2$-depleted and $H_2S$-containing profundal zone. Chaoborus appears either during the Sergentia or the Chironomus phase, but can also remain absent. p.55

The same criteria — improvement of nutritive conditions, deterioration of oxygen conditions — were used in the attempt to explain the vertical migration of Lauterbornia coracina, Sergentia coracina, Calopsectra, and Chironomus. For the two first-mentioned species, increased temperatures were considered as the causative factor.

There are several facts which deviate from LUNDBECK's concept:

1. Sergentia coracina migrates into the profundal zone simultaneously with Lauterbornia, but then persists there longer, so that, at times, the

impression of a "Sergentia-lake" may arise. However, in Great Ploen Lake, both species were wiped out at the same time. 2. The Tanytarsus community consists of a number of species which, ecologically, are markedly different: In the Schöhsee, Lauterbornia is wiped out as early as during the Atlantic stage, other Tanytarsus species continue to play an important part, and Calopsectra is just starting to really penetrate the profundal zone during the Subboreal stage. Even now, Tanytarsus and Calopsectra larvae still exist in the pedonic strata of the Schöhsee.

on p.5

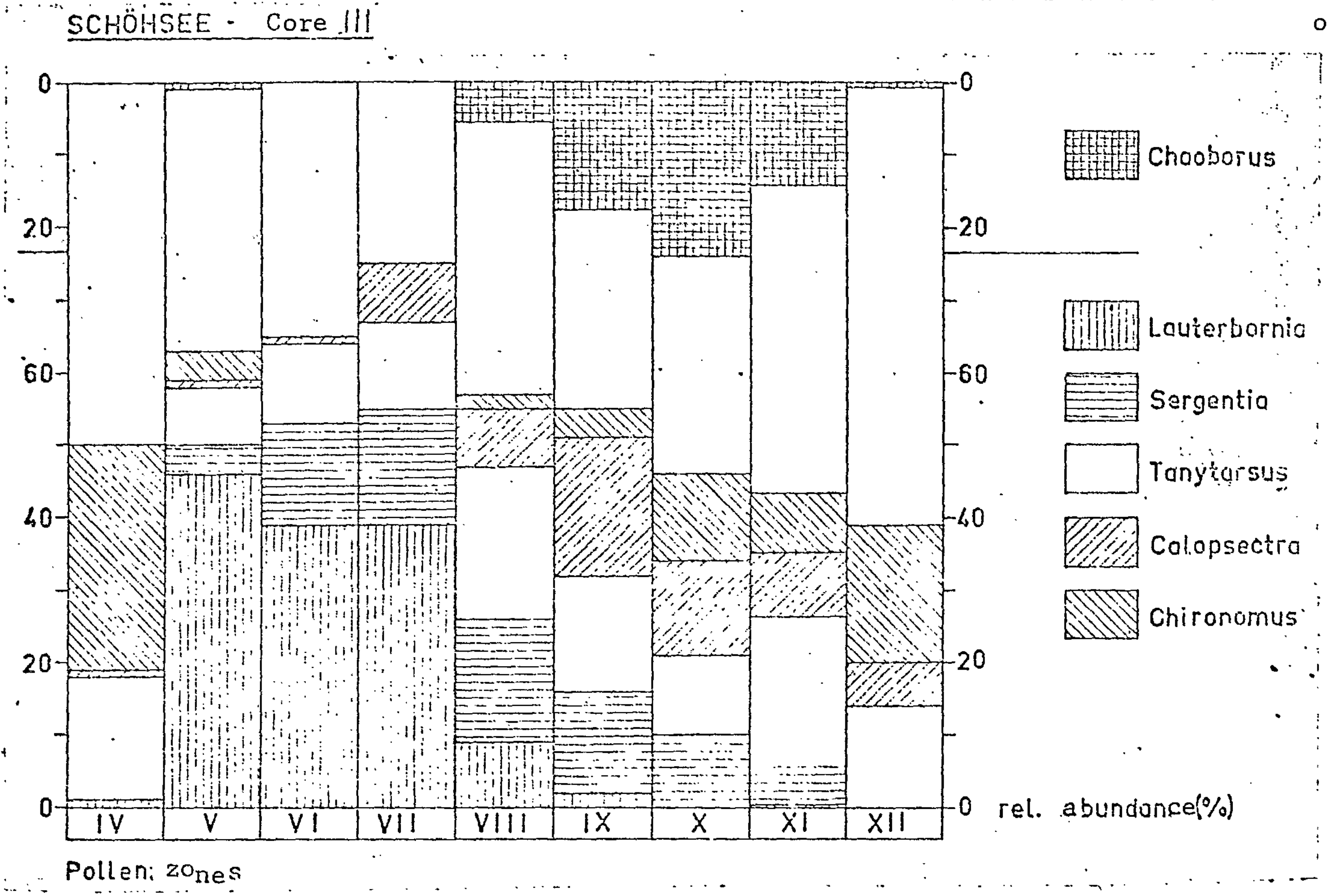

Fig. 22: Schöhsee, core III; relative abundance of the most frequent Chironomidae, and of Chaoborus flavicans during the climatic stages.

This is also the most serious objection brought forth against the authors of the lake-type concept: The characterization of the profundal zone had always been based on "larva-types", but never — except for *Chironomus* — on species (WÜLKER 1961a : 307-309). Generally, it was quite clear which species was predominant in the profundal zone of the oligotrophic crater lakes of the Eifel region (THIENEMANN 1915), and the North German "*Tanytarsus* lakes" (THIENEMANN 1920): *Lauterbornia coracina*. But despite this, the formulation "*Tanytarsus* lake" is kept in use and has caused much confusion. If "*Tanytarsus*" is taken to stand for Tanytarsini — and this is what the term was meant to denote — there is no way of knowing which genus it is supposed to designate. It may just as well be presumed that the author refers to species of the genus *Tanytarsus*, which is, in fact, not the case (cf. PAGAST 1941 : 388, 393-397). Even more difficult is the case of LUNDBECK's "*Orthocladius* lake." It was unknown which Orthocladiinae species occupied the deep alpine lakes and the Scandinavian lakes. It was assumed that the eurybathic Orthocladiinae in the "Vättern" (Lake Vatter, Sweden) investigated by EKMAN (1915) were identical with *Psectrocladius*, while, actually, they represent *Heterotrissocladius subpilosus* (BRUNDIN 1949 : 468-469).

It was just as doubtful which species characterize the "*Sergentia* lake" and the "*Stictochironomus* lake." The results were contradictory because first one and then the other species was referred to: For *Stictochironomus* it was *histrio* at one time, and *rosenschöldi* at another, for *Sergentia* there were *coracina* and *longiventris*. These are species which are distinctly different in their ecological attitudes (BRUNDIN 1949 : 639-648; cf. LENZ 1927).

BRUNDIN (1949b, 1956b) deserves credit for establishing a solid foundation for the definitions "*Orthocladius* lake" and "*Tanytarsus* lake." p.56 The characterizing species, at least for the Scandinavian "ultraoligotrophic" lakes, is *Heterotrissocladius subpilosus*; beside this, *Pseudodiamesa nivosa* may also be of importance (BRUNDIN 1949 : 661-663; 1956 : 192-202).

The species which characterize the profundal zone of "moderately oligotrophic" lakes have been combined by BRUNDIN (1949 : 664) to form the *Stictochironomus rosenschöldi* community, which he later extends and renames *Tanytarsus lugens* community (BRUNDIN 1956 : 203). This includes the following:

*Protanypus morio*
*Monodiamesa bathyphila*
*Heterotrissocladius grimshawi*
*Heterotrissocladius määri*
*Paracladopelma obscura*
*Sergentia coracina*
*Stictochironomus rosenschöldi*
*Micropsectra insignilobus*
*Lauterbornia coracina*
*Tanytarsus lugens*

Regarding the eutrophic lakes, BRUNDIN (1956 : 209) confirms the traditional concept (THIENEMANN 1915, 1918; LENZ 1925; LUNDBECK 1926, 1936): "Here is only to be emphasized that the eutrophic lakes of the entire holarctic region have a profundal fauna among which the large *Chironomus* larvae play, quantitatively, an outstanding role."

Upon application of this latest status of research on bottom-faunal lake types, as formulated by BRUNDIN (1949, 1956), to the results of the present investigation, the development of the Schöhsee presents itself as follows: Schöhsee (and the same is true of Great Ploen Lake) has never been an ultraoligotrophic lake with *Heterotrissocladius subpilosus* in its profundal zone. Instead, right from the beginning, the profundal zone was occupied by members of the *Tanytarsus lugens* community (except for the lower profundal zone during the later Dryas stage with its Chironomus population). The following leading forms have been detected in Lake Schöhsee:

| | |
|---|---|
| Protanypus | |
| Monodiamesa | Sergentia coracina |
| Heterotrissocladius grimshawi | Stictochironomus |
| Paracladopelma obscura | Lauterbornia coracina |

According to BRUNDIN (1949 : 652), the Stictochironomus head capsules from the older sediments would belong to the species Stictochironomus rosenschöldi. It should be mentioned also that the species Tanytarsus lugens is to be found among the Calopsectra head capsules. In all, a total of eight taxa of the Tanytarsus lugens community have therefore been established as having been present in the Schöhsee at that time.

It is true, however, that the chronological distribution and the frequency of the enumerated species are subject to great variations. Protanypus, Monodiamesa, Heterotrissocladius grimshawi, and Paracladopelma obscura have been found only in limited numbers in the oldest sediments, primarily during the later Subarctic and Preboreal stages. Only Heterotrissocladius grimshawi plays, here, quantitatively a more important p. 57 role. Lauterbornia coracina and Sergentia coracina, on the other hand, are frequent profundal inhabitants over long periods of time. Lauterbornia is the predominant Chironomidae genus in the pedonic strata during the Preboreal and Boreal stages, in Great Ploen Lake even until the Subboreal stage.

Until Subboreal I, the profundal zone of the Schöhsee is characterized by the species of the Tanytarsus lugens community, and, according to BRUNDIN, the lake would have to be considered as "moderately oligotrophic." During that time, Chironomus still occupies the sublittoral zone. Chaoborus appears in the pedon in greater numbers already during the Atlantic stage.

The phase from Subboreal II to Subatlantic I can be depicted as transitional stage: Sergentia is still represented in the profundal zone, and Chironomus begins its vertical migration.

The next step is the Chironomus'lake: Chironomus anthracinus is the predominant Chironomidae species in the profundal zone. In 1924, LUNDBECK (1926) found the lake precisely in this condition.

Due to progressing deterioration of the oxygen conditions and to secondary nutrient deficiency of the sediment, the Chironomidae, especially the Chironomus species were since, to a very great extent, forced out of the profundal zone.

The classification of the phases of the lake's development, introduced above, namely: Moderately oligotrophic phase / transitional phase / eutrophic phase, is meant to demonstrate the application of the lake types formulated by BRUNDIN (1949, 1956). The important difference between his system and that of LUNDBECK (1926, 1936) and LENZ (1925, 1927) is the absence of an intermediary mesotrophic type, between the eutrophic and the oligotrophic types; the species which are supposedly characteristic of this transitional type, Sergentia coracina and Stictochironomus rosenschöldi, are included by BRUNDIN in his Tanytarsus lugens community. During the history of the Schöhsee and that of Great Ploen Lake, Sergentia coracina behaves basically very much like Lauterbornia coracina. This fact supports the concept of BRUNDIN.

## XI. Distribution-ecological aspects

### Critical prefatory remarks

From the start, application of the results to animal geography is subject to the same limitations as their application to existence-ecology.

It is there also of great disadvantage that most Chironomidae could not be classified further than to their genus. Just as it is the species that copes with its environment, it is as much the species which, under changing conditions, increases or decreases the area of its distribution. The basic element in all zoogeographical considerations is the species-specific area (cf. DE LATTIN 1967 : 61-72). Therefore, only those p.58 taxa can here be taken into consideration whose classification includes the species.

The fact that a certain genus exists in a certain region does not say much if it is unknown which of its species are involved. However, if evidence is available that in a certain region or during a certain period of time this genus (that is, all the species belonging to this genus) is not present, this is an important finding. From this point of view, it is meaningful if -- for example -- the absence of a certain genus during the late glacial and early postglacial times can be established with some degree of probability, because this would mean that all species of this genus now living in the area have migrated to it only during the postglacial period.

In this connection, one fact especially must be pointed out: In this investigation, it is of major interest to learn in what manner the newly-formed lake gradually became inhabited. If the head capsules of one taxon are found only in the Boreal and younger layers, the negative findings in the older sediments are not of decisive importance in existence-ecological considerations, because the main question is: When does the species have its optimum? The important factor in solving zoogeographical problems is whether the negative results prior to the Boreal stage constituted conclusive evidence of the absence of this species. In any case, the statement that a certain species is not present in a specific area is permissible only after detailed knowledge of all the appropriate biotopes has been gained. So little is known about the chorology of the Chironomidae that, in "Limnofauna europaea" (ILLIES 1967 : 346-381) it could be stated with certainty only in the case of a single species that it were not represented in certain regions. For the purpose of compiling a list of all species belonging to the family of the Chironomidae in a lake that stretches over an area of 75 hectares, one would hardly screen the sublittoral and profundal sediments from four locations in search for head capsules. The recent fauna can be determined on hand of a collection of larvae, pupal cases, and imagoes. For the subfossorial fauna, the only useful method is the one outlined here; its shortcomings can be compensated to a certain degree by including as much material as possible. For example, from Subboreal I of core I, a total of 1,413 head capsules were recovered; but this included also four taxa represented only by one specimen each (relative abundance = 0.07%). It is therefore quite certain that still rarer taxa exist which have not yet been recovered even with this large material. On the other hand, the utmost limit of a reasonable amount of work has been reached so that this degree of closeness to the facts will have to suffice.

If the existence of a given species cannot be denied with certainty even in one particular lake, it is all the more difficult to do so with reference to a large territory, e.g., Holstein or North Germany. Therefore, all negative findings reported in connection with this investigation will have to be viewed with critical reservation.

Still another difficulty arises from the zoogeographical evaluation: The discussion of the ecology of the species could be based on already existing grounds; a great amount of information is available from the literature. However, the exact range of distribution, for example, has yet to be established for practically all Chironomidae species. p. 59

With regard to their fauna, the most thoroughly investigated lakes are the Swedish lakes, particularly those of South Sweden (BRUNDIN 1949). Of Great Ploen Lake, which is "with regard to its Chironomidae fauna the best investigated lake outside of Sweden" (BRUNDIN 1949 : 593), only 75% of the existing species are known, as estimated by HUMPHRIES (1938 : 539).

The great variation in the numbers of species in the zoogeographical areas of Europe do not reflect the true situation, but are the effect of uneven intensity in the collection of material (ILLIES 1966 : 290).

Since a general animal geography for the Chironomidae is still lacking, there is practically no point of reference for the views on the history of distribution of this family that resulted from this investigation. They can be related to the postglacial "History of Dispersion of the Fresh-Water Fauna in Europe" ("Verbreitungsgeschichte der Süsswassertierwelt Europas;" THIENEMANN 1950, cf. ILLIES 1964), but the special problems of individual Chironomidae species are not deducible on that basis. THIENEMANN, although being a specialist on Chironomidae, mentions only few of the species and these mainly in connection with the boreo-alpine distribution type.

## The primary populations

During the later Dryas stage, already 30 of the 49 taxa here distinguished were present. Taking even into consideration that a somewhat warmer period had already existed (Alleroedian*), it can still be postulated that the pioneer communities were recruited mainly from the northern forms of the subterminal glacier species and elements of the glacial mix-faunae(cf. THIENEMANN 1950 : 337-379, 394-423; ILLIES 1964 : 174-179), namely:

*Pentaneurini* part.
*Procladius*

*Cricotopus* A
*Cricotopus* B
*Heterotrissocladius grimshawi*
*Monodiamesa*
*Parakiefferiella bathophila*
*Protanypus*
*Psectrocladius*
Gen.? *triquetra*
*Chironomus*
*Cryptocladopelma*
*Dicrotendipes*
*Glyptotendipes*
*Microtendipes*
*Pagastiella orophila*
*Parachironomus*
*Paracladopelma obscura*
*Polypedilum*
*Sergentia coracina*
*Stictochironomus*

*Calopsectra* part.
*Cladotanytarsus*
*Corynocera ambigua*
*Lauterbornia coracina*
*Paratanytarsus*
*Stempellinella*
*Tanytarsus* B
*Tanytarsus heusdensis*-Kr.
*Tanytarsus* part.

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Eight of the ten Orthocladiinae taxa, and nine of the twelve Tanytarsinae taxa are already accounted for, but only eleven out of twenty-four of the Chironomini taxa, that is, the latter are relatively the least represented taxa. The recession of the Chironomini in northern highland and high alpine regions is a typical phenomenon: THIENEMANN (1950 : 347) established that the Chironomidae characteristic of the northern highland region (Abisko, Sweden) consist of 73% Orthocladiinae, and only of 6% Chironomini. Many of the Chironomini genera are missing in alpine lakes above 1,000 m (REISS 1968a : 124).

BRUNDIN (1949 : 610-612) characterizes the Swedish range of the species listed, as follows (for <u>Monodiamesa</u> and <u>Protanypus</u> both possible species are listed):

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*) <u>Translator's note</u>: Alleroedion period, after the Danish town "Alleröd," later Pleistocene until middle of Subarctic period = appr. 10,000 to 9,000 B.C.

In northernmost Sweden (in arctic and subarctic lakes only):

*Cricotopus alpicolus* (BRUNDIN: sub-*Paratrichocladius*; here: sub-*Cricotopus* B part.)
*Protanypus caudatus*

In northern Sweden, relicts extending all the way to South Sweden:

*Monodiamesa ekmani*
*Paracladopelma obscura*
*Sergentia coracina*
*Lauterbornia coracina*

Boreal species in Sweden, which probably extend their continuous distribution into Småland:

*Heterotrissocladius grimshawi*
*Monodiamesa bathyphila*
*Protanypus morio*
*Corynocera ambigua*

Related to all Europe, two distribution-types become manifest (BRUNDIN 1949, THIENEMANN 1950, WÜLKER 1958, ILLIES 1967):

Boreal range:

*Monodiamesa ekmani*
*Protanypus caudatus*
*Corynocera ambigua*

Boreo-alpine range:

*Cricotopus alpicolus*
*Heterotrissocladius grimshawi*
*Monodiamesa bathyphila* p. 61
*Protanypus morio*
*Pagastiella orophila*
*Paracladopelma obscura*
*Sergentia coracina*
*Lauterbornia coracina*

However, of these, only *Cricotopus alpicolus* and *Paracladopelma obscura* have not been found in the intermediate area (secondary mountain chain [Harz Mountain group] and North German low plain) so that only these are typical boreo-alpine species (THIENEMANN 1950 : 529). The others are designated by THIENEMANN (1950 : 530) as boreo-alpine in a broader sense. According to their origin, the former are called sessile, the latter progressive subterminal glacier species (ILLIES 1964 : 174-179).

All pioneer populations whose systematics have been defined as far as the species, have now a northern boreo-alpine (s.str. or s.l.*) European range. In cold areas they are littoral inhabitants, in temperate lakes they dwell in the profundal zone, which indicates cold-oriented stenothermia. This is further substantiated by the fact that the species in arctic-subarctic lakes eclose during summer, and those in Central Europe during spring (some shortly after the ice breaks up) and autumn (cf. BRUNDIN 1949).

## The postglacial newcomers

The statements made in this chapter are based on negative findings in older sediments. In view of this, the above-mentioned reservations are re-emphasized.

During the Preboreal stage, Cryptochironomus, Pseudochironomus, and Tanytarsus C were observed for the first time. In the sediments of Boreal I, Corynoneura, Endochironomus tendens, Einfeldia, Lenzia, and Stempellina appear.

Endochironomus tendens is a far-ranging littoral species which, according to BRUNDIN (1949 : 748) is missing from subarctic inland waters, according to REISS (1968a : 124) from Alpine lakes above 1,000 m. This and the fact that, in Småland (BRUNDIN loc.cit.) and in Great Ploen Lake (HUMPHRIES 1938 : 563-564, sub-Endochironomus albipennis), eclosion takes place during summer, show that it is a warmth-oriented form.

Microcricotopus bicolor, Paracladopelma species, Paralauterborniella nigrohalteralis, and Stenochironomus appear during Boreal II.

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*) Translator's note: s.str. or s.l. = sine structura or sine loco: without indication as to details or place (in short: no reference supplied by author who was cited).

BRUNDIN (1949 : 612-614, 709-710) calls Microcricotopus bicolor a Pan-Scandinavian species whose continuous range extends into subarctic regions. From "Limnofauna europaea" (ILLIES 1967 : 361) it becomes clear that the species is found all over Europe. It is missing in Alpine lakes over 1,000 m (REISS 1968a : 122-123). In Småland (BRUNDIN loc.cit.), in p.62 Great Ploen Lake (HUMPHRIES 1938 : 562), and in Lake Constance (REISS 1968b : 241) eclosion takes place during summer.

Paralauterbornia nigrohalteralis is not found in the subarctic lakes (BRUNDIN 1949 : 765), nor in the Alps above 1,000 m (REISS 1968a : 122-123). The species has a wide range of distribution in Europe; but it is unknown throughout the secondary mountain chains (ILLIES 1967 : 374). It occurs also in the USA and in Canada (BRUNDIN loc.cit.). In Småland (BRUNDIN loc.cit.), in Lake Usma (Courland, Latvia) (PAGAST 1931 : 230), and in Lake Constance (REISS 1968a : 262-263), Paralauterbornia nigrohalteralis is a summer-form. BRUNDIN (1949 : 548) classifies it as mildly warmth-orientated species.

Of the three known European Stenochironomus species, St. gibbus extends as far as the high boreal region (BRUNDIN 1949 : 776-777). The genus is absent in the Alps above 1,000 m (REISS 1968a : 124). All species are summer-forms (BRUNDIN 1949 : 776-777; HUMPHRIES 1938 : 564; REISS 1968b : 268).

New additions in Atlantic sediments are Paratendipes and Xenochironomus xenolabis. In core GPS II, the former is present as early as during the Preboreal stage. Six species of this genus are known within the area (ILLIES 1967 : 374); no comment is therefore necessary. Of Xenochironomus xenolabis only a single head capsule was recovered. Although this chance finding is quite inconclusive, it should be mentioned that this species has been detected in Scandinavia only in Småland (BRUNDIN 1949 : 780), and does not occur in the Alps at elevations above 1,000 m (REISS 1968a:124). The season for eclosion is during summer (BRUNDIN l.c.; REISS 1968b : 269).

Until Subboreal I, 47 of the 49 taxa have made their appearance; new arrivals are Labrundinia longipalpis and Thienemanniola.

Only four specimens of Labrundinia longipalpis were recovered. The locations where the species is found point to a North European range of distribution: Finland, Sweden (Småland and Jämtland), England, Belgium (BRUNDIN 1949 : 680-681, sub-Ablabesmyia; FITTKAU 1962 : 381; ILLIES 1967 : 348). However, it is certainly not a "northern" species: It has since been found also in Romania (ALBU & BOTNARIUC 1966 : 50; ALBU 1966 : 145); in Sweden and Finland, it is found only in marsh areas which indicates a relict distribution (FITTKAU 1962 : 374). It is a summer-form (BRUNDIN 1949 : 597-598). Furthermore, longipalpis is the only European species of a genus whose main distribution is in subtropic and tropic regions (FITTKAU loc.cit.): All this tends to support the opinion that the species migrated into the area only during the postglacial warm period.

The fact that Thienemanniola was not encoutered in sediments from the later Dryas to the Atlantic stages (in total, 2,377 head capsules were recovered), but that it was present with great regularity and sometimes even in considerable abundance (relative frequency up to 18%) from the Subboreal period on, indicates that this Chironomidae species indeed appears only then in the Schöhsee where it found an unoccupied ecological niche. Unfortunately, little is known about Thienemanniola: It p. 63
is not certain whether the three species described by KIEFER (1921a : 87;

1921b : 327; 1924 : 44) should be maintained (cf. ILLIES 1967 : 376; question mark); information about the distribution of the genus is full of gaps. Until recently, Great Ploen Lake and Lake Uklei were thought to be the only places where it could be found. In the spring of 1968, REISS (oral communication) found imagoes at Great Ploen Lake and Lake Selent (Schleswig-Holstein, Germany). Just recently, the presence of the genus was reported from the area of Lake Stechlin (see MOTHES), and from Bohemia (Czechoslovakia) (see LELLAK [ref.not listed] material in the Ploen collection). The imagoes swarm about the water surface and are therefore hard to catch. It is remarkable, nevertheless, that Thienemanniola is unknown in so well-sampled areas as Sweden (BRUNDIN) or the Alps with the Alpine fotthills (THIENEMANN, REISS). Since nearly always the pupal cases were also taken into consideration, the genus should have been detected. The pupae are hardly to be mistaken for any other Chironomidae species (nor the imagoes either). Therefore, if its range in Europe is really that limited, this could be due to its very late appearance.

The two Chironomidae which showed up last (not before Subboreal II) are Demicryptochironomus and Lauterborniella agrayloides.

According to LENZ (1954-1962 : 224), the species vulneratus ZETTERSTEDT and ploenensis LENZ belong with certainty to the genus Demicryptochironomus. The former has been classified by BRUNDIN (1949 : 612-614, 744) as an eurythermal Pan-Scandinavian species. It is widely distributed throughout Europe (ILLIES 1967 : 371, sub-Cryptochironomus; REISS 1968b : 253). In Småland (BRUNDIN loc.cit.) and in Lake Constance (REISS loc.cit.) it occurs as a summer-form. The presence of Demicryptochironomus ploenensis has been evidenced only for Great Ploen Lake and the Lago Maggiore (North Italy - South Switzerland) (LENZ 1954-1962 : 224; 1959; ILLIES 1967 : 371, sub-Cryptochironomus). The time of eclosion is summer (LENZ loc.cit.).

In Europe, Lauterborniella agrayloides has a decidedly Central-European range of distribution: South Sweden, South Finland, Germany = Holstein, East Prussia (now Poland/USSR), Eifel region, Pfalz (Palatinate), BÜhmen-MÄhren (Bohemia and Moravia, Czechoslovakia), Holland, England (in addition USA, Canada) (BRUNDIN 1949 : 751). The species is missing in northern Scandinavia as well as in the Alps and the Alpine foothills (cf. ILLIES 1967 : 372). BRUNDIN (1949 : 548) considers it to be mildly warmth-oriented stenothermal. It ecloses during summer (BRUNDIN 1949 : 751).

## Primary population and postglacial newcomers — different faunal elements

The essence of the above, unfortunately rather generalized, zoogeographical characterization is the interesting grouping of the Chironomidae species:

Those that lived in the lake as early as during the later Dryas stage have now in Europe a boreal range of distribution, or a boreo-alpi- p. 64
ne distribution in a strict or in a broader sense (cf. THIENEMANN 1950 : 529-530). The modern boreal and typically boreo-alpine species are, regarding their origin, considered to be sessile subterminal glacier species (THIENEMANN 1950 : 337-394; ILLIES 1964 : 174-179). Species which are boreo-alpine in a broader sense count as progressive subterminal glacier species (THIENEMANN loc. cit.; ILLIES loc. cit.). They form the littoral population in subarctic lakes, and eclose during summer; in temperate lakes, they are limited to the profundal zone, and eclose during spring and autumn (cf. BRUNDIN 1949).

Sixteen additional taxa appear one by one in the sediments until Subboreal II. It seems justified to infer from this fact that these Chironomidae migrated to this area only during postglacial times, especially since all well-defined taxa are more ore less warmth-orientated species. This is substantiated by their modern range of distribution (absent in the Subarctic and in the Alps above 1,000 m; for one genus, the main range of distributian are the Tropics and Subtropics), but also by the fact that the season of eclosion is during summer. It can be assumed that, during the later Dryas stage when the subterminal glaciers followed appr. the Oslo-Aland Islandsline, these Chironomidae had not yet entered the North German terrain but lived farther south, or in one of the large glacial refugia (cf. DE LATTIN 1967 : 218-219). Primary populations and postglacial newcomers are, therefore, two different faunal elements.

Extinct species

While new species settle in the lake during the postglacial warm period, many of the pioneer populations are wiped out. In the sediments of Subatlantic II, from which 2,591 head capsules had been recovered, eight of the 49 taxa were no longer in evidence. One of these, Einfeldia, is according to investigations by SCHLEE (unpublished) still present in the lake. Lauterborniella agrayloides and Xenochironomus xenolabis, although there is no evidence for their presence in the Schöhsee, have been observed in neighbouring lakes: L. agrayloides in the Krummensee (BRUNDIN 1949 : 751), X. xenolabis in Great Ploen Lake, see LENZ (ref. not cited, material in the Ploen collection). Corynocera had still been observed at Great Ploen Lake in 1922 by THIENEMANN (1954 : 460), but has never again been found since then.

Furthermore, there are species which were still recovered from sediments of Subatlantic II but, as long as Chironomidae research has been conducted in the area, these were no longer found; there are also those species (+) whose hypopygia were found in older sediments, and which are no longer part of the recent fauna. Also to be mentioned is *Cricotopus alpicolus* of which one specimen was reliably identified in sediments from the Preboreal period (see HIRVENOJA); because of the difficulties in identification, the presence of this species among the head capsules from younger sediments was questionable, but *C. alpicolus* is now no longer present in the area. p. 65

A provisional list of extinct species would include the following:

*Labrundinia longipalpis*
*Cricotopus alpicolus*
*Heterotrissocladius grimshawi*
*Protanypus*
Orth. gen.? *triquetra* (?)
*Pagastiella orophila*
*Paracladopelma obscura*
*Sergentia coracina*
*Corynocera ambigua*
*Lauterbornia coracina*
*Paratanytarsus penicillatus*
*Tanytarsus niger*

All the species are boreo-alpine or boreal forms, except *Labrundinia longipalpis* (Orth. *triquetra* cannot be discussed because of the taxonomical difficulties). Most taxa have already been characterized in the chapter on "primary populations."

One boreal species has been designated as *Paratanytarsus penicillatus* by BRUNDIN (1949 : 611-612, 791-792); its continuous range extends as far as Småland. In subarctic lakes, the period of eclosion begins in June, in Småland it starts in spring. The species is known only in northern Europe.

*Tanytarsus niger* was hitherto found only in East Greenland (ILLIES 1967 : 380), but its presence has now been established also in Lake Stechlin by MOTHES (1966 : 260). The two last-mentioned species thus complete the series of sessile and progressive subterminal glacier species.

The Chironomidae which were classified as boreo-alpine and boreal according to their recent range of distribution, have therefore initially occupied the intermediate area during late glacial and postglacial times, but were then wiped out in the course of time; this resulted in a range reduction or disjunction.

### Remarks concerning range disjunction of some Chironomidae

It could be demonstrated that several species which were present in the Schöhsee and Great Ploen Lake as early as during late glacial times, became extinct during the postglacial period. With the exception of *Labrundinia longipalpis*, these are the same species that were classified as boreo-alpine and boreal forms by diverse authors, according to their present range of distribution.

One of them is *Lauterbornia coracina*, which is, according to THIENEMANN (1950 : 539) a boreo-alpine species in the broader sense. In the p. 66
profundal zone of the Schöhsee it is by far the most abundant Chironomidae species until Boreal II, and is still present in the lake until Subatlantic I; in the profundal sediment of Great Ploen Lake it contributed 25-40% of the Chironomidae head capsules until Subboreal I (appr. 1000 B.C.): the species survives in limited numbers at least until Subatlantic I. The discussion of the ecological factors involved has shown that, in all probability, the species has been driven away because of the declining hypolimnetic oxygen supply.

A similar situation exists in the case of *Sergentia coracina*: It is frequent in both lakes until Subboreal II, and has still been found in Schöhsee-sediments during Subatlantic II, and in Great Ploen Lake during Subatlantic I. At this lake, it was still observed even by THIENEMANN (1954) in the year 1918. Its recent distribution is interpreted by WÜLKER (1958, 1961a) as a glacial disjunction; in agreement with this, the communities in South Sweden and Central Europe are considered as glacial relicts by BRUNDIN (1949 : 611, 653).

Apart from the boreal and alpine distribution of Lauterbornia coracina, this species is widely distributed throughout Central Europe: North German plains = Mecklenburg (Schalsee, Breiter Lucin, Lake Stechlin); Pomerania (Lake Dratzig, Lake Madue); Poland (Lake Wigry, Lake Hancza); Eifel region (in the crater lakes Gemündener Maar, Pulvermaar, Weinfelder Maar, and Laacher See); High Tatra, Czechoslovakia (HRABĚ 1939 : 1-3; BRUNDIN 1949 : 786; THIENEMANN 1950 : 539; MOTHES 1966b : 89-90). Apparently, this species is present with such regularity in all Central-European lakes which have an oxygen-rich hypolimnion that THIENEMANN (1915, 1918) calls it the "characterspecies" for oligotrophic lakes.

Sergentia coracina also occurs in numerous locations within the discontinuous region: South Sweden, Holstein (Garensee), Mecklenburg, Pomerania, Masurian Lakes, Poland (Lake Wigry, several lakes in the Warta district near Poznan), Black Forest, Vosges Mountains (WÜLKER 1961a : 326-328).

The distribution ranges of both these species are very similar. The only difference is that Sergentia does not occur in the Eifel region. WÜLKER (loc.cit.) showed that all places where the species is found are located within the boundaries of maximal glaciation. Despite the fact that the shortest distance between the two ranges is only about 500 km (Poznan-Lunz), the range of Sergentia shows a boreo-alpine disjunction. However, in this intermediate area, the deep oligotrophic lakes are very much missing .

(or have not yet been investigated); the only exceptions are the crater lakes of the Eifel region. This "discontinuity of the biotope" makes it extremely difficult to evaluate the areal disjunctions. A direct dependency of the existence of a species upon hypolimnetic $O_2$-content has been established by THIENEMANN (1920, 1928) in North Germany and the Warta district, so that, here, the species seems to exist in all those biotopes that offer a suitable environment.

The following applies to *Lauterbornia coracina* and *Sergentia coracina*: The Central-European range is extensive, neither is it small with p. 67
respect to the boreal and alpine distribution; the species are not distributed randomly throughout the area but are present in all biotopes where they can be expected from an existence-ecological point of view (exception: the absence of *Sergentia* from the crater lakes of the Eifel region). The communities in the respective lakes are not any small relict populations but represent the predominant Chironomidae of the profundal zones (cf. HARNISCH 1925; DE LATTIN 1967 : 33); regression of the ranges begins only very late during the postglacial period.

The frequency of two other species, deemed as boreo-alpine, namely *Heterotrissocladius grimshawi* and *Paracladopelma obscura*, is reduced already during early postglacial times; they have their optimum during the later Dryas and Preboreal stages. In the sediment of Great Ploen Lake, isolated specimens only were found also during later periods.

While, in Sweden, the range of *Heterotrissocladius grimshawi* extends continuously to Småland (BRUNDIN 1949 : 611-612), it is rarely found in the discontinuity zone in Central Europe: Ardennes (BRUNDIN 1949 : 704), and Black Forest (WÜLKER 1958 : 810). *Paracladopelma obscura* leads only a "relictoid existence" in South Sweden (BRUNDIN 1949 : 610-611) and is completely absent from the remaining intermediate area.

viewpoints which resulted from the investigation of the subfossorial Chironomidae. However, first of all, it was to be demonstrated that the method employed here can contribute important facts to enlighten the history of distribution of this animal family.

## XII. Summary

The Schöhsee has a depth of 30 m and covers an area of 79 hectares. During summer stagnation, oxygen depletion occurs regularly below 15 m. The pedonic fauna of the profundal zone is characterized by massive amounts of Tubificidae and a high abundance of Chaoborus flavicans. The Chironomidae (Polypedilum nubeculosum, Chironomus anthracinus, Calopsectra, Tanytarsus) are, by comparison, far less numerous. The sublittoral zone is inhabited by Chironomus anthracinus, Chironomus plumosus, Monodiamesa bathyphila, Procladius, and Polypedilum nubeculosum. p. 68

The subfossorial head capsules of Chironomidae larvae, and the mandibles of Chaoborus larvae were recovered from four sediment cores obtained from the Schöhsee (at depths of 10 m, 12 m, 22 m, 26 m), and from one sediment core taken from Great Ploen Lake (depth 41 m); the subfossorial material was picked out from random samples of 1 ml of fresh sediment each. Pollen-analytical dating of the cores was on hand. Except for core II from the Schöhsee, all borings covered sediments up to the later Subarctic stage.

The methods employed for the isolation and preparation of the subfossorial material are described.

The total mean of head capsules/ml of sediment was: 25 in Schöhsee-cores I and II, 21 in core III, and 29 in core IV. High fossil density was detected in the sediments from the later Dryas stage. It decreases until the Atlantic stage, then increases again until Subboreal II, and declines once more in recent times.

Only 18 of the 49 taxa (Chironomidae and *Chaoborus flavicans*) show a distinct maximum in their frequency at a given time.

As early as during the Preboreal-Boreal stages, the frequency of *Protanypus*, *Heterotrissocladius grimshawi*, and *Paracladopelma obscura* decreases. Abundance maxima during the Atlantic-Subboreal stages were noted for *Procladius*, *Einfeldia*, *Calopsectra*, *Corynocera ambigua*, and *Chaoborus flavicans*. Most frequently present in recent sediments were: *Cricotopus* A, *Endochironomus tendens*, *Endochironomus intextus*, *Paratendipes*, *Cladotanytarsus*, and *Thienemanniola*. Two abundance maxima — one in the oldest, the other in the most recent sediments — were observed for *Chironomus*, *Microtendipes*, *Tanytarsus* B. The results from a comparative study of the core from Great Ploen Lake (GPS II) were basically the same in all respects.

Migration into the profundal zone was evidenced in the case of (in chronoligal order): *Lauterbornia coracina*, *Sergentia coracina*, *Calopsectra*, and *Chironomus*. Thereby, the frequency of *Lauterbornia* decreases markedly already during the Atlantic stage, that of *Sergentia* during the Subboreal period.

*Chaoborus flavicans* appears during the Atlantic stage in greater numbers in the profundal zone; maximal abundances were observed during the Subboreal stage and during Subatlantic I.

The vertical migration of *Sergentia* and *Lauterbornia* is interpreted as a consequence of the postglacial temperature increase. The disappearance of *Protanypus*, *Heterotrissicladius grimshawi* and *Paracladopelma obscura*, the decimation of *Lauterbornia* and *Sergentia*, and the appearance of *Chaoborus flavicans* and *Chironomus* in the profundal zone are all attri- p.69

buted to a reduction of the hypolimnetic oxygen content and the saturation of the profundal sediment with nutritive substances.

In connection with the fluctuations in the frequency of Chaoborus flavicans, the humus-factor is discussed. The humic acid content of the sediment is correlated with the number of mandibles per ml of sediment.

The lake-type theory of BRUNDIN (1949, 1956) is applied to the succesions in the profundal zone. Neither of the two lakes was ever an Orthocladius-lake. A Tanytarsus lugens community is replaced, after a transitional period (Subboreal II-Subatlantic I), by Chironomus. These circumstances indicate a moderately oligotrophic phase, an intermediate period, and a eutrophic phase.

All primary populations, that is, taxa which existed already during the later Dryas stage, have now -- as far as the species can be defined -- a boreal or boreo-alpine distribution. In the subarctic region they eclose during summer, in North and Central Europe during spring and autumn.

The postglacial migrants are now absent throughout the subarctic region and in the Alps above 1,000 m elevation. In Central Europe, they eclose during summer.

A list of extinct species has been compiled.

The eutrophication of lakes as a causative factor for areal regression, particularly the boreo-alpine disjunction, is discussed.

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