INTRODUCTION

ABSTRACT

RESULTS

STUDY

Lake

DANISH SPECIES GROUPINGS

EUTROPHIC LATE-GLOacial MOST 840

VALUES

Atlantic lake (an eutrophic, "clay"

Atlanlic time was due to unstable conditions within the lake, evidenced by deposition of sand; Chydorus piger was abundant during this period. Sub-Boreal organic deposits overlay the Atlantic sands. High percentages of Pleuroxus during mid-Sub-Boreal were attributed to man's activity, and a lower water level. The most recent change in chydorid assemblages occurred within the past 100 yrs; this change was increased percentages of Alona nana—a species normally associated with low alkalinitities in Denmark.

Postglacial calcareous gyttja deposits in Esrom Sø extended to 380 cm below the mud-water surface interface. Calcareous clay extended from 381-840 cm, and glacial till occurred below 840 cm. Pollen preservation was poor in Esrom, but the lowermost gyttija was probably Pre-Boreal (Zone IV). No pollen counts were attributable to Zone VI. Few chydorid remains were found in Late-glacial clays, and extensive development of populations began in Pre-Boreal time (370 cm). Chydorid assemblages characteristic of discriminant Group 1 were present throughout most of the postglacial deposits; benthic species were prevalent during most of the lake's history. Littoral forms did increase in Sub-Boreal time, but by Sub-Atlantic chydorid assemblages were again dominated by benthic groups.

In Esrom, postglacial chydorid fluctuations were dampened by its morphological and chemical characteristics, while Grane Langsø fossil assemblages were sensitive to minor variations in the lake's environs. Pioneer chydorid species in northern Europe are Chydorus sphaericus, Alona affinis, A. quadrangularis, Acroperus harpae, and Alona nana.

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Species Groupings

Species Diversity

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INTRODUCTION

Chydorids are of great value in paleolimnological studies, because they leave fossil remains identifiable to species. These remains can be recovered easily from the sediments, usually in sufficient quantities for statistical analysis. The habits of present-day species have been studied by Fryer (1963, 1968), Smirnov (1962, 1963a, 1963b, 1964, 1966), and Flössner (1967) and, except for a study by DeCosta (1964), very little effort has been made to examine the regional relations between chydorid species and lake types. Furthermore, no attempts have been made to apply results of a regional study to paleolimnological interpretations of lake sediments from the same region. For these reasons, knowledgeable interpretations of a lake's past ecological condition, based on remains found in cores of lake sediment, are somewhat limited. This study explores some of the ecological relationships found between chydorid species and lake types in Denmark and applies the results to interpretations of cores of sediments from two Danish lakes.

Section I of this paper deals with present-day chydorid populations from 80 Danish lakes. These lakes represent a wide spectrum of lake types, ranging from the highly oligotrophic Grane Langsø to the "ultra"-eutrophic Fredriksborg Slotsø (Dunn, 1954). Size ranges from small bogs and ponds to lakes as large as 4063 ha. The wide variety of lakes in a compact geographic area reduces those variables associated with latitude and altitude and eliminates some of the problems encountered by DeCosta (1964), who worked over a latitudinal range of 17 degrees. Climate, a major factor in chydorid distributions (DeCosta, 1964; Harmsworth, 1968), has been eliminated as a variable because of the relative uniform climatic conditions over the study area. This allows for a more informative approach to other factors important in the ecology of chydorids. Furthermore, since Danish lakes have been fairly well described by numerous limnologists (Table 1), they are ideal for the study of present-day chydorid faunas.

Section II in this study presents the results of core studies from two Danish lakes, Grane Langsø and Esrom Sø. These two lakes were chosen for study because their differences were reflected in the lake ontogeny.

SECTION II: PRESENT-DAY CHYDORID ASSEMBLAGES

METHODS

During July 1965 surficial sediments were collected from 80 Danish lakes following the techniques of DeCosta (1964). One sample was taken with an Ekman dredge from the offshore benthic area of each lake. The dredge was raised to the surface with maximum care so that the original mud surface remained undisturbed. The uppermost 2-3 cm of mud were carefully placed in a plastic bag, and formalin was added. Collections of live Cladocera were made in the littoral zone of each lake studied. From these two types of collection, lists of chydorid species were made for each lake; any major differences between species lists based on live samples and those derived from dredge samples are mentioned in the Species Analysis Section.

The sediment samples were processed by methods modified from those of Frey (1960, 1961). Approximately 5 g of sediment was heated in 5% KOH for 15-20 min on a hotplate equipped with a magnetic stirrer. The sample was then screened through a bronze 250-mesh screen to remove silts, clays, and KOH solution. A weak solution of HCl was then added to remove carbonates. The residue, which contained animal microfossils, plant fragments, and sand, was placed in a copper beaker, to which 5-10% HF was added. The beaker was heated on the hot-plate for 5 min. This procedure removed a majority of the sand particles. Following a final rinse in tap water through the screen, the residue was concentrated in vials to a volume of 15 ml. From this volume, which was equivalent to a known amount of sediment, 0.05-ml aliquots were transferred to slides and mounted in glycerine jelly beneath 22-mm coverslips. Counts of chydorids were made at a magnification of 100X. Each remain, whether head shield, shell, or post-abdomen, was counted as one animal. Each species is readily recognizable from any one of these parts. Listings of the relative abundances of the chydorids in each lake were punched on IBM
cards for statistical analysis by the CDC 3600 computer at the Indiana University Research Computing Center.

In each lake studied, a liter of water was obtained from the off-shore limnetic area for determining transparency and conductivity. When data on alkalinity were lacking, this parameter was also measured.

Transparency was measured as per cent transmittance with a Beckman DU 2400 spectrophotometer using 10-cm cells at 360 m\(\mu\) from a blue light source. A first measurement was made on the raw water taken directly from the 1-liter sample. A second was made on lake water that had been centrifuged for 3 min. The difference between these two transmittance values for a given lake, which depends primarily on the amount of suspended material in the water, is the \(d\) value. The principal factors affecting this value are discussed in more detail later (Species Analysis).

All conductivity measurements were made on the July 1965 water samples with a Radiometer (Copenhagen), type CDM2, at 20°C.

The estimates of primary production given in Table 1 were kindly provided by Dr. P. M. Jónason, who gathered the data from various sources (Steemann Nielsen, 1958; Jónasson and Mathiesen, 1959; Jónasson, 1963, 1964, 1965; Mathiesen, 1962, and Kristiansen and Mathiesen, 1964). These estimates have been corrected by a factor of 1.45, as suggested by Steemann Nielsen (1965). The productivity estimate from Lille Gribsø (28), provided by Aage Rebsdorf, was based on measurements he made during 1966–1967.

In Skovsø (62) and Sortedam (65) tree leaves covered the bottom to such an extent that representative mud samples were impossible to obtain. For this reason these lakes have been omitted from all statistical analysis. A third site, Bøndernes Mose (10), was also omitted, since it is a senescent bog not comparable to the lakes. The remaining 77 lakes were used in calculating chydorid species abundance and defining lake typology.

**Study Area**

Denmark is a lowland country composed of the peninsula of Jutland, the principal islands of Zealand, Fyn, Bornholm, Lolland, Færoes, and several hundred smaller islands. The lakes (Fig. 1) studied are located in Jutland and Zealand exclusively, between the parallels 54°05’N and 57°45’N and the meridians 8°04’E and 12°40’E. This is a total of approximately 40,000 km². The climate is normally milder than one would expect at this latitude due to the Gulf Stream, and only occasionally are harsh periods of continental climate felt. Annual precipitation is between 50 and 75 cm, with most of the precipitation from January to March in the form of snow. The relatively mild, wet climate, coupled with the uneven, rolling glacial topography of low relief, has given rise to numerous lakes.

The present landscape of Denmark has resulted largely from the inland ice masses and meltwater rivers associated with the Glacial Age; pre-Quaternary deposits have had little direct influence on the forms of present-day land surfaces (S. Hansen, 1965). During the Pleistocene the most recent (Würmian) glaciation had the most influence in forming the present-day land features. The Würmian ice did not cover the entire land area of Denmark as had the earlier glaciers. West and south of about 9°20’E Long. (the Main Stationary Line of Madsen, 1928) the basic topography dates from the Russian glaciation. There the surface forms have been subjected to a radical leveling process—a consequence of solifluxion—during the Würmian period (Milthers, 1948).

The landscape here is mainly heath-plies interrupted by hills. Some extensive outwash plains resulting from the Würmian meltwater occur just west of the Main Stationary Line.

Four lakes were sampled south and west of Würmian moraines. Fåresø (23), Grovsø (30), and Praestesø (55), located in Würmian fluvial-glacial deposits, are shallow, with low alkalinitates and generally low pH (Table 1). They are probably typical of the calcium-poor soils of this area. A fourth lake, Filso (15), is also located in this area, but it is situated on marine deposits along the west coast. It is more typical of Danish eutrophic lakes, except that it has a fairly low alkalinity and a somewhat lower pH range (Table 1).

East and north of the Main Stationary Line the glacial landforms are still in a youthful stage. Steep hills, tunnel valley systems with extramarginal valleys, and other features indicate former drainage conditions. Thirty-five of the lakes studied owe their origin to these tunnel valleys, and 28 of these occur in Jutland; in Zealand the subglacial rivers gave rise to eskers instead (Hansen, 1965a). A wide physical and chemical diversity exists among these lakes (Table 1).

Only 9 Jutlandic lakes were classified as morainic lakes on till. All except Skanderborg Sø (61) are acidic and small.
In southwestern Zealand the ice of the Great Belt stage of the Würmian glaciation advanced from the west and southwest. In northeastern Zealand the ice came from the east, forming the ridges in northwest Zealand and in the forests of Gribskov. In contrast to the Jutlandic lakes, most lakes of Zealand are morainic in origin: 25 of the 30 sampled. In general the smaller lakes are similar to those found in Zealand, i.e. they are acidic and mainly bog-like. These are typified by Lille
### Table 1. Summary of the physical, chemical, and biological characteristics of the 80 Danish lakes studied

| Lake number | Lake, Origin, and Type | Area (ha) & Max. Depth (m) | Transparency (%) | Color | Conductivity (μS/cm) | pH & Alkalinity Range (meq/L) | Primary Productivity (av. g C/m²/yr.) | Species Diversity Index | References |
|-------------|------------------------|----------------------------|------------------|-------|----------------------|-------------------------------|----------------------------------------|------------------------|-----------|
| 1.          | Almindøs               | 54                         | 88.1             | 2     | 175                  | 6.4-7.7                       | 62                                      | 3.78                   | 3, 12, 14, 18, 20, 29, 30, 34, 37, 39, 40, 46, 48, 54, 59 |
|             | TV, 1                  | 20                         | 89.5             | 10    | 12 H                 | 0.54-1.06                     |                                        |                        |            |
| 2.          | Arresø                 | 4063                       | 15.0             | 11 O  | 350                  | 6.8-8.6                       | 1.58-2.19                              | 1.60                   | 3, 11, 30, 46 |
|             | MA-G, 3                | 4                          | 40.3             |       |                      |                               |                                        |                        |            |
| 3.          | Bagvaerød Sø           | 121                        | 6.5              | 8     | 325                  | 6.5-10.1                      | 522                                    | 1.23                   | 3, 15, 25, 29, 37, 38, 69, 66 |
|             | TV, 3                  | 4.5                        | 39.9             | 40 H  | 70 H                 | 2.36-3.30                     |                                        |                        |            |
| 4.          | Baneise Sø             | 56                         | 46.5             | 600   |                      | 8.1-9.0                       | 305                                    | 2.03                   | 17, 18, 19, 33, 59 |
|             | TV, 3                  | 8                          | 48.5             |       |                      | 3.5-4.0                       |                                        |                        |            |
| 5.          | Blegø                  | 44                         | 55.0             |       |                      | 6.2-8.5                       | 3.55                                   | 22, 23, 24, 31, 37, 40, 48 |
|             | MA, 1                  | 6                          | 58.0             |       |                      | 0.6-1.1                       |                                        |                        |            |
| 6.          | Bondedam               | (14.8)                     | 10.5             | 11 O  | 270                  | 6.3-8.0                       | 3.35                                   | 1.2, 3                 |            |
|             | MO, 2                  | 3                          | 11.2             | 7 C   |                      | 1.4                           |                                        |                        |            |
| 7.          | Borresø                | 202                        | 58.8             | 15 H  | 270                  | 8.0-9.2                       | 392                                    | 1.59                   | 14, 18, 20, 34, 37, 39, 48 |
|             | TV, 3                  | 8                          | 60.1             | 18 H  |                      | 1.8-1.9                       |                                        |                        |            |
| 8.          | Brøndtøs               | 107                        | 57.3             | 20 H  | 258                  | 8.6-9.2                       | 1.47                                   | 12, 59                 |            |
|             | TV, 1                  | 14                         | 65.0             |       |                      | 1.7-1.8                       |                                        |                        |            |
| 9.          | Bøgøholm Sø            | (39.5)                     | 6.0              | 7 C   | 255                  | 6.9-7.5                       | 2.06                                   | 1, 2                   |            |
|             | MO, 2                  | 2                          | 6.5              | 10 C  |                      | 1.3                           |                                        |                        |            |
| 10.         | Bondenerøs Mose I      | ca 6 m²                   | 0.0              | 114 O | 198                  | 3.7-4.2                       | 0.08                                   | 3, 30, 37, 40, 41 |
|             | MO, 2                  | 0                          | 0.0              |       |                      |                               |                                        |                        |            |
| 11.         | Donne Støredam         | (15)                       | 22.5             | 22 O  | 377                  | 7.7                           | 3.13                                   | 3, 30                  |            |
|             | MO, 2                  | ca 2.5                     | 23.5             |       |                      | 1.8-2.7                       |                                        |                        |            |
| 12.         | Ellertøs               | 6.3                        | 15.8             | 50 H  | 210                  | 7.5-8.8                       | 266                                    | 2.27                   | 37         |
|             | TV, 1                  | ca 2                       | 26.3             |       |                      | 0.9-1.4                       |                                        |                        |            |
| 13.         | Eresø Sø               | 1730                       | 75.5             | 4 O   | 322                  | 7.4-8.7                       | 261                                    | 2.81                   | 3, 4, 14, 15, 18, 20, 21, 26, 27, 28, 29, 30, 37, 38, 40, 46, 59 |
|             | MO, 1                  | 21                         | 78.0             | 3 O   |                      | 2.0-2.5                       |                                        |                        |            |
| 14.         | Farum Sø               | 121                        | 33.9             | 419   |                      | 6.7-8.5                       | 471                                    | 2.20                   | 37, 38, 60 |
|             | TV, 3                  | 16                         | 49.0             |       |                      | 4.0                           |                                        |                        |            |
| 15.         | Fjelts                  | 85                         | 30.5             | 40 O  | 295                  | 6.8-7.3                       | 1.74                                   | 3, 54                  |            |
|             | MA, 3                  | 1                          | 48.1             |       |                      | 1.2                           |                                        |                        |            |
| 16.         | Flade Sø               | 561                        | 61.1             | 8 O   | 1800                 | 8.0-9.0                       | 1.19                                   | 3, 24, 31, 54 |
|             | MA, 1                  | ca 2                       | 67.1             |       |                      | 2.4                           |                                        |                        |            |
| 17.         | Flynderøs              | 483                        | 50.2             | 11 O  | 290                  | 7.2-9.0                       | 2.39                                   | 3, 46, 55, 54 |
|             | TV, 3                  | ca 4                       | 62.0             |       |                      | 1.4                           |                                        |                        |            |
| 18.         | Frederiksholb Søtøn    | 22                         | 14.5             | 8 O   | 330                  | 7.2-9.7                       | 560                                    | 0.05                   | 3, 8, 14, 15, 18, 21, 29, 30, 35, 37, 38, 39, 40, 41, 42, 46, 59 |
|             | MO, 3                  | 3                          | 36.2             |       |                      | 2.7                           |                                        |                        |            |
| 19.         | Fumkedam               | (2)                        | 26.1             | 20 O  | 329                  | 7.0-8.1                       | 2.89                                   | 3, 30, 40            |
|             | MO, 2                  | ca 3                       | 27.0             |       |                      | 2.0                           |                                        |                        |            |
| 20.         | Furesø                 | 506                        | 67.8             | 1 O   | 338                  | 6.8-8.8                       | 312                                    | 3.08                   | 3, 11, 12, 13, 14, 15, 21, 28, 30, 32, 36, 37, 38, 39, 40, 41, 42, 46, 59, 60 |
|             | TV, 1                  | 38                         | 69.2             | 4 O   |                      | 2.2-2.4                       |                                        |                        |            |
|             |                       |                            |                  | 8 H   |                      |                               |                                        |                        |            |
| 21.         | Fusing Sø              | 200                        | 79.4             | 4 O   | 308                  | 9.0                           | 3.39                                   | 3                      |            |
|             | TV, 1                  | ca 19                      | 80.1             |       |                      | 1.9                           |                                        |                        |            |
| Lake number | Lake, Origin, and Type | Area (ha) | Depth (m) | Trans-parency (%) | Conductivity (μS cm⁻¹) | pH & Alkalinity (meq L⁻¹) | Primary Productivity (av. g C/m²/yr.) | Species Diversity Index | References |
|-------------|-----------------------|----------|-----------|-------------------|------------------------|---------------------------|----------------------------------------|------------------------|------------|
| 22.        | Fjæstrup Dam          | (4)      | 13,5      | 60 O              | 310                    | 7.0-8.1                   | 3.9                                    | 2.45                   | 3, 20, 40  |
| 23.        | Færesæ                 | 7.1      | 63.8      | 64 O              | 100                    | 5.7-6.8                   | 3.49                                   | 40, 54                 |            |
| 24.        | Gadsø Store            | .4       | 0.0       | 38 O              | 133                    | 6.3-8.7                   | 2.36                                   | 3, 30                  |            |
| 25.        | Geddersæ               | 3.3      | 91.5      | 12 H              | 70                     | 4.1-4.8                   | 2.52                                   | 40, 48                 |            |
| 26.        | Glenstrup Sø            | 354      | 64.0      |                   | 333                    | 8.0                       | 2.53                                   | 53                     |            |
| 27.        | Grecse                 | 11       | 92.1      | 5 H               | 49                     | 4.9-5.9                   | 80                                    | 14, 18, 20, 22, 29, 33, 39, 42, 43, 44, 55 |
| 28.        | Gule Sø                 | 243      | 17.6      | 8 O               | 365                    | 0.2-8.8                   | 1.45                                   | 2, 3, 4, 23, 30, 34, 39 |
| 30.        | Grenøe                  | 4.1      | 52.0      | 12 O              | 175                    | 5.4-6.8                   | 2.77                                   | 3, 39, 40              |            |
| 31.        | Gurre Sø                | 243      | 17.6      | 8 O               | 365                    | 0.2-8.8                   | 1.45                                   | 2, 3, 4, 23, 30, 34, 39 |
| 32.        | Hald Sø                 | 134      | 344       | 85.9              | 243                    | 7.2-9.0                   | 2.72                                   | 3, 40, 54              |            |
| 33.        | Hampen Sø               | 26       | 76        | 5 O               | 78                     | 5.4-8.5                   | 3.54                                   | 3, 18, 19, 23, 30, 33, 40, 41, 48, 54 |
| 34.        | Hinge Sø                | 26       | 152       | 15 H              | 275                    | 8.2                       | 1.86                                   | 3                      |            |
| 35.        | Hjortøen                | 36       | 76        | 5 O               | 78                     | 5.4-8.5                   | 3.54                                   | 3, 18, 19, 23, 30, 33, 40, 41, 48, 54 |
| 36.        | Store Hjulsø            | 35       | 344       | 85.9              | 243                    | 7.2-9.0                   | 2.72                                   | 3, 40, 54              |            |
| 37.        | Store Hulsø             | 26       | 76        | 5 O               | 78                     | 5.4-8.5                   | 3.54                                   | 3, 18, 19, 23, 30, 33, 40, 41, 48, 54 |
| 38.        | Hundøe                  | 26       | 76        | 5 O               | 78                     | 5.4-8.5                   | 3.54                                   | 3, 18, 19, 23, 30, 33, 40, 41, 48, 54 |
| 39.        | Juleøe                  | 36       | 76        | 5 O               | 78                     | 5.4-8.5                   | 3.54                                   | 3, 18, 19, 23, 30, 33, 40, 41, 48, 54 |
| 40.        | Kaløe Sø                | 26       | 76        | 5 O               | 78                     | 5.4-8.5                   | 3.54                                   | 3, 18, 19, 23, 30, 33, 40, 41, 48, 54 |
| 41.        | Klaersø                 | 36       | 76        | 5 O               | 78                     | 5.4-8.5                   | 3.54                                   | 3, 18, 19, 23, 30, 33, 40, 41, 48, 54 |
| 42.        | Klestrup Sø             | 26       | 76        | 5 O               | 78                     | 5.4-8.5                   | 3.54                                   | 3, 18, 19, 23, 30, 33, 40, 41, 48, 54 |
| 43.        | Knapøe                  | 36       | 76        | 5 O               | 78                     | 5.4-8.5                   | 3.54                                   | 3, 18, 19, 23, 30, 33, 40, 41, 48, 54 |
| 44.        | Køberdam               | 36       | 76        | 5 O               | 78                     | 5.4-8.5                   | 3.54                                   | 3, 18, 19, 23, 30, 33, 40, 41, 48, 54 |

Table 1.—Continued
Table 1.—Continued

| Lake number | Lake, Origin, and Type | Area (ha. & Max. Depth (m)) | Transparency (%) | Conductivity (R200) | pH & Alkalinity Ranges (meq) | Primary Productivity av. & C/m²/yr. | Species Diversity Index | References |
|-------------|-----------------------|-----------------------------|------------------|---------------------|-------------------------------|-------------------------------------|--------------------------|------------|
| 45.         | Kalø                  | 46                          | 62.7             | 155                 | 6.0-7.2 .92                  | 2.66                                | 54                       |            |
| 46.         | Lyngby Sø             | 60                          | 60.5             | 7 O                 | 343 7.4-9.8 3.05-3.90         | 355 1.86                            | 11, 15, 18, 21, 25, 29, 30, 35, 38, 39, 40, 49 |
|             | TV, 3                | 2                           | 65.5             | 30 H                |                               |                                      |                          |            |
|             |                      |                             |                  | 70 H                |                               |                                      |                          |            |
| 47.         | Langø                 | (3.5)                       | 18.5             | 9 O                 | 168 6.0-7.9 .60              | 3.03                                | 3, 15, 30, 37, 48         |            |
|             | MO, 2                | 4                           | 20.0             |                     |                               |                                      |                          |            |
| 48.         | Madam Sø              | 212                         | 88.9             | 4 O                 | 98 4.6-5.2 .05-.08           | 3.46                                | 3, 23, 30, 37, 40, 54 |
|             | MO, 1                | 7                           | 88.9             |                     |                               |                                      |                          |            |
| 49.         | Mossø                 | 588                         | 67.4             | 7 O                 | 310 8.0-9.0 1.4-2.1          | 0.92                                | 15, 30, 40, 41, 48, 59 |
|             | TV, 1                | 21                          | 69.1             |                     |                               |                                      |                          |            |
| 50.         | Mossø (Roldskov)      | (5.5)                       | 0.0              | 192 O               | 93 4.0-4.2 .19               | 3.22                                | 30, 37                 |
|             | MO, 2                | 6                           | 0.0              |                     |                               |                                      |                          |            |
| 51.         | Nors Sø               | 337                         | 89.0             | 2 O                 | 223 7.8-8.3 .94-2.0          | 3.31                                | 3, 18, 23, 24, 31, 37, 40, 41, 44, 46, 54 |
|             | MA, 1                | 9                           | 82.0             |                     |                               |                                      |                          |            |
| 52.         | Nørresø               | 124                         | 43.0             |                     | 255 7.5-8.7 1.1              | 1.13                                | 28, 59                 |
|             | TV, 3                | 12                          | 59.5             |                     |                               |                                      |                          |            |
| 53.         | Ove Sø                | (500)                       | 37.5             | 10 O                | 498 6.3-9.0 1.30-2.98        | 2.36                                | 3, 24, 31, 54           |
|             | MA, 1                | 2                           | 36.9             |                     |                               |                                      |                          |            |
| 54.         | Pederborg Sø          | 19                          | 11.4             | 40 H                | 303 7.0 2.56                | 0.41                                | 25, 26, 38, 39, 51      |
|             | MO, 3                | 6.5                         | 31.8             |                     |                               |                                      |                          |            |
| 55.         | Præstø Sø             | 10                          | 46.8             | 10 O                | 160 7.9-9.0 .23              | 3.46                                | 3, 16, 30, 40, 41, 58 |
|             | G, 2                 | 1                           | 49.2             |                     |                               |                                      |                          |            |
| 56.         | Ravnsø                | 183                         | 66.0             | 4 O                 | 358 9.0 1.82                | 3.24                                | 3                     |
|             | TV, 1                | 33                          | 66.9             |                     |                               |                                      |                          |            |
| 57.         | Ribeøerg Sø           | 12                          | 10.0             | 25 O                | 243 6.4 2.91                | 23, 30                 |
|             | MA, 2                | 2                           | 12.1             |                     |                               |                                      |                          |            |
| 58.         | Salten Langø          | 128                         | 69.1             | 18 H                | 195 7.4-8.5 1.06-1.30        | 2.28                                | 12, 40, 41, 48, 50     |
|             | TV, 1                | 12                          | 79.0             |                     |                               |                                      |                          |            |
| 59.         | Silkeborg Langø       | 235                         | 42.0             |                     | 171 7.5-8.8 .94              | 1.64                                | 39, 64                 |
|             | TV, 3                | 4.9                         | 30.9             |                     |                               |                                      |                          |            |
| 60.         | Speløs Sø             | (300)                       | 16.8             | 13 O                | 400 7.7-9.0 1.29-2.38        | 1.16                                | 3, 9, 30               |
|             | MO, 3                | 3                           | 31.5             |                     |                               |                                      |                          |            |
| 61.         | Skanderborg Sø         | (870)                       | 57.7             | 6 O                 | 345 7.7-9.0 2.09-2.09        | 1.22                                | 3, 15, 30, 39, 50     |
|             | MO, 1                | 18.8                        | 62.0             |                     |                               |                                      |                          |            |
| 62.         | Skovø                 | (50 m²)                     | 17.0             | 8 O                 | 367 6.7-6.9 1.14              | 1.07                                | 3, 30                 |
|             | MO, 2                | .75                         | 17.0             |                     |                               |                                      |                          |            |
| 63.         | Silæsø                | 18.2                        | 91.0             | 10 H                | 212 7.2-8.0 1.23-2.15        | 1.14                                | 3, 14, 20, 33, 37, 39, 41, 48 |
|             | TV, 1                | 11.5                        | 91.3             | 15 H                |                               |                                      |                          |            |
|             |                      |                             |                  | 5 H                 |                               |                                      |                          |            |
| 64.         | Sønder-Igelsø         | 3                           | 82.8             | 49                  | 6.8-7.0 .14-.26              | 3.53                                | 30                     |
|             | TVE, 1               | 7                           | 83.9             |                     |                               |                                      |                          |            |
| 65.         | Sorø Sø               | ( .3)                       | 24.4             | 112 O               | 383 6.3-8.0 .64              | 1.75                                | 30, 37, 40, 41         |
|             | MO, 2                | 1                           | 24.9             |                     |                               |                                      |                          |            |
| 66.         | Sorø Sø               | 3.4                         | 2.0              | 15 O                | 155 5.0-6.3 .19              | 2.98                                | 1, 2, 30, 40          |
|             | MO, 2                | 6                           | 2.2              |                     |                               |                                      |                          |            |
| 67.         | Sørs Sø               | 217                         | 33.6             | 10 O                | 267 7.7-8.5 2.16-2.27        | 5.89                                | 3, 25, 26, 30, 37, 38, 40, 46, 51, 59 |
|             | MO, 3                | 13                          | 54.0             | 25 H                |                               |                                      |                          |            |
| Lake number | Lake, Origin\(^1\) and Type\(^2\) | Area (ha) & Max. Depth (m) | Transparency\(^3\) (%) | Color\(^4\) | Conductivity (\(\text{R}_{20}\)) | pH & Alkalinity Ranges (meq) | Primary Productivity (av. g C/m\(^2\)/yr.) | Species Diversity Index | References\(^6\) |
|-------------|----------------------------------|--------------------------|------------------------|----------|-------------------------|-----------------------------|---------------------------|----------------------|-----------------|
| 68. | Steinholt Sø | 2.3 & 11 | 88.2 & 88.2 | | 72 & | 4.6 & | 3.71 & | | |
| 69. | Selved Sø | 15 & 7 | 44.9 & 44.9 | | 780 & | 8.1-10.4 & | 566 & 5.9 & | | |
| 70. | Sønderø | 151 & 7 | 38.0 & 49.2 | | 415 & | 8.3-9.0 & | 0.58 & 2.1 & | | |
| 71. | Thorø | 64 & 8 | 73.5 & 75.3 | | 190 & | 6.5-8.6 & | 138 & 3.65 & | | |
| 72. | Tisse | 1352 & 18 | 32.0 & 580 | | 8.4-8.8 & | 2.78 & | | | |
| 73. | Tjøle Langø | 471 & 16.6 | 33.1 & 295 | | 8.0-9.0 & | 0.76 & | | | |
| 74. | Tuel Sø | 191 & 19 | 44.0 & 550 | | 6.7-8.2 & | 9.1 & 3.05 & | | |
| 75. | Tystrup Sø | 662 & 16 | 45.5 & 620 | | 7.5-9.0 & | 4.93 & 2.02 & | | |
| 76. | Vester Vanned Sø | 450 & 20 | 84.0 & 313 | | 6.3-9.0 & | 1.89 & | | | |
| 77. | økans | 3.2 & | 79.5 & 54 | | 8 & | 3.43 | | 30 |
| 78. | ørens | 42.5 & 10.5 | 62.5 & 18 H | | 7.1-9.1 & | 2.84 & | | | |
| 79. | Lille økans | 0.0 | | | | | | | | |
| 80. | Store økans | 44 & 7 | 22.7 & 90 O | | 4.0-5.2 & | 2.01 | | | |

\(\text{NVygard}, 1965.\)  
\(^1\text{Origin coded as follows: TV=tunnel valley, TVS=tunnel valley (extramarginal), MA=marine, MO=morainic, G=glacial (undefined).}\)  
\(^2\text{Type coded as follows: 1=clear water, 2=peats and bogs, 3=polished clear-water.}\)  
\(^3\text{Transparency given as 2 readings; the upper value is transmittance through uncentrifuged water, while the lower reading shows transmittance through water centrifuged for three minutes.}\)  
\(^4\text{Color coded as follows: O=Oleje, H=Hansen degrees, C=Carmel units.}\)  
\(^5\text{Reference numbers refer to numbered references at end of Table 1.}\)  
\(^6\text{Reference S-new approximation of size.}\)
Gribsø and Store Gribsø (28 & 29), Hjortesøle (35), Klæresø (41), Løgøsø (47), and Sortesø (66). However, some Zealandic morainal lakes, including Esrom Sø (13), Tissø (72), and the Sorø lakes (54, 67, & 74), have been polluted or have calcium-rich waters.

A third group of lakes is found along the coastal margins. One of these, Filsø (15), has already been mentioned. These lakes have complex origins. They all lie on postglacial marine deposits on landscapes recently uplifted from the sea. In some instances glacial deposits form a portion of the shoreline. Included in this group are the Jutlandic lakes Blegesø (5), Flade Sø (16), Nors Sø (51), Ove Sø (53), Råbjaerg Sø (57), Vester-Vanned Sø (76), and Danmarks largest lake, Arresø (2). Of these lakes Jensen (1958) regards Blegesø, Nors Sø, and Vester-Vanned Sø as karst lakes. This term is used with some reservation, for although the lakes are in contact with limestone bedrock, they are not typical of lakes found in karst regions. Their present configuration is controlled primarily by the recent glaciation and the post-glacial marine deposits.

Table 1 represents a compilation of physical, chemical, and biological data from many sources, supplemented in some instances by measurements made during July 1965. The precision of these data depend on the source. Hence it is best not to rely on a single kind of measurement but to evaluate the lake from the composite of information provided. For more detailed information regarding any lake the reader is referred to the references given in Table 1. The numbers arbitrarily assigned to each lake are consistent throughout the text, tables, and figures.

**RESULTS**

**LAKE GROUPINGS**

The purpose of this study was to investigate possible relations between lake types and the presence and abundance of chydorid species. One approach is to arrange chydorid species associations within acceptable, well-defined lake types—analagous to the direct gradient analysis of Whittaker (1967). Another is to form lake groups based on the similarities and differences of species composition of the lakes. The direct analysis has been used in this study.

Lakes as a class constitute a multidimensional continuum in which it is difficult to establish groups. The most reasonable approach to grouping is to select characters that have the greatest range of differences among the lake types, but even with this method difficulties arise if the number of lakes is large, for differences may be gradational through the entire range. The most desirable method to describe lake types would be a multi-dimensional ordination system, but this method does not seem feasible at the present time.

For the purpose of this study I have formed 3 lake groups based on 7 chemical-physical parameters: (1) clear-water lakes, (2) ponds and bogs, and (3) culturally affected clear-water lakes (loosely referred to as polluted). Ponds and bogs are distinct lake types, but because of the similarity of their chydorid assemblages and the fact that only 6 bogs were sampled, the two types were placed in a single group. Within each lake group 5 of the 7 parameters (transparency, conductivity, pHmin, and alkalinitymin) are interrelated (Tables 2–4). High transparency is normally associated with the CaCO₃ available at the locality (see Species Analysis for further discussion). The

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**Table 2. Correlation coefficients among selected lake parameters in the clear-water Danish lakes**

| Parameter       | Trans- | d    | Conduct. | pHmin. | Alkal. | Species Diversity |
|-----------------|--------|------|----------|--------|--------|-------------------|
| Transparency    | 1.00   |      |          | -0.49**| -0.21  | -0.01             |
| d               | 1.00   | 0.24 |          | 0.30   | -0.14  | -0.68**           |
| Conductivity    | 1.00   |      | 0.85**   | -0.08  | -0.08  | -0.44*            |
| pHmin.          | 1.00   |      |          | 0.78** | -0.40* |                   |
| Alkalinitymin.  | 1.00   |      |          |        | -0.45* |                   |
| Species Diversity|       |      |          |        |        | 1.00              |

*significant at p=0.05; **significant at p=0.01.

**Table 3. Correlation coefficients among selected lake parameters in the pond and bog group**

| Parameter       | Trans- | d    | Conduct. | pHmin. | Alkal. | Species Diversity |
|-----------------|--------|------|----------|--------|--------|-------------------|
| Transparency    | 1.00   | 0.37 |          | -0.09  | -0.35  | 0.42              |
| d               | 1.00   | 0.17 | 0.34     |        | 0.22   | 0.00              |
| Conductivity    | 1.00   |      | 0.80**   | 0.02   |        | -0.02             |
| pHmin.          | 1.00   |      |          | 0.70** | 1.00   | -0.13             |
| Alkalinitymin.  | 1.00   |      |          |        | 1.00   |                   |
| Species Diversity|       |      |          |        |        | 1.00              |

**significant at p=0.01.**

**Table 4. Correlation coefficients among selected lake parameters in the polluted clear-water lakes**

| Parameter       | Trans- | d    | Conduct. | pHmin. | Alkal. | Species Diversity |
|-----------------|--------|------|----------|--------|--------|-------------------|
| Transparency    | 1.00   |      |          | -0.70**| 0.19   | 0.36              |
| d               | 1.00   |      |          | -0.38**| 0.43   | -0.31             |
| Conductivity    | 1.00   |      |          | 0.24   | -0.12  | -0.44             |
| pHmin.          | 1.00   |      |          | 0.12   | 1.00   | -0.03             |
| Alkalinitymin.  | 1.00   |      |          |        |        | 1.00              |
| Species Diversity|       |      |          |        |        |                   |

**significant at p=0.01.**
three lake groups display the following general relationships for the 7 parameters (means are given in parentheses):

**Clear-water lakes:**
- Transparency (%)—high, usually greater than 50% ($\bar{x} = 69.7\%$).
- $d$—low ($\bar{x} = 2.7$).
- Conductivity ($K_{20}$)—low, usually less than 250 micromhos ($\bar{x} = 280.9$).
- pH$_{min}$—about 7.0 ($\bar{x} = 6.9$).
- Alkalinity$_{min}$—low, usually about 1.0 meq ($\bar{x} = 1.2$).
- Maximum depth—usually greater than 10 m ($\bar{x} = 15.5$).
- Area—variable, usually greater than 10 ha ($\bar{x} = 346.9$).

**Ponds and bogs:**
- Transparency—in ponds a wide range (0–91%), but in bogs usually less than 22% ($\bar{x} = 27.4\%$).
- $d$—low ($\bar{x} = 0.9$).
- Conductivity—low ($\bar{x} = 171.8$).
- pH$_{min}$—low in bogs and some ponds ($\bar{x} = 5.6$).
- Alkalinity$_{min}$—low in bogs and most ponds ($\bar{x} = 0.7$ meq).
- Maximum depth—shallow ($\bar{x} = 3.3$ m).
- Area—small ($\bar{x} = 7.5$ ha).

**Polluted lakes:**
- Transparency—low, usually less than 50% ($\bar{x} = 33.3\%$).
- $d$—high ($\bar{x} = 12.8$).
- Conductivity—high, usually greater than 250 ($\bar{x} = 382.3$).
- pH$_{min}$—slightly higher than in clear-water lakes ($\bar{x} = 7.5$).
- Alkalinity$_{min}$—high ($\bar{x} = 2.3$ meq).
- Maximum depth—shallower than clear-water lakes ($\bar{x} = 7.6$ m).
- Area—variable ($\bar{x} = 396.4$ ha, range 6.3–4063 ha).

There are exceptions to the general scheme outlined above. For instance, Store Økssø (80), although classified as a pond, has a fairly large area (44 ha) and depth 7 m. This lake is unique in its water color (low transparency) and other parameters, so it is characterized better as a pond than as a lake. There are many other lakes within groups which, for any one character, may not fit well into their group range. These exceptions, as mentioned earlier, are due to the multidimensional nature of a lake.

The validity of this subjective grouping of lakes was tested by multiple discriminant analysis (Fisher, 1936), which emphasizes the differences among the lake groups on the basis of the 7 measurements. This approach also provides an efficient basis for examining the nature of any differences found, and it provides equations that can be used for predicting (Cooley and Lohnes, 1962, Ch. 6).

A discriminant analysis enables the following operations to be performed: 1) One can test the multivariate null hypothesis that the means of these three lake groups are the same for all seven variables with the use of Wilk's Lambda criterion. 2) Each parameter can then be tested individually between lake groups using single variable analysis of variance procedures, and F ratios can be calculated. 3) The scaled vector values assigned to each parameter are the relative weight assigned to each variable in the discriminant function; a variable with a large scaled vector is relatively "important" in determining lake type. 4) The groups are defined by group centroids on the basis of the discriminant scores, and these can be plotted to illustrate graphically the differences between groups. 5) A probability value is assigned to each lake, according to the discriminant score obtained from the lake parameters. The probability value of a lake indicates which group it is most like according to its discriminant score; one expects clear-water sites to have the highest probabilities of occurring in the clear-water group (Group 1), ponds and bogs to have the highest p-values in their group (Group 2), and polluted sites to have the largest p-values in the polluted lake group (Group 3).

A discriminant analysis, using a computer program slightly modified from Cooley and Lohnes (1962) by C. J. Krebs, was carried out on the 77 Danish lakes divided into the three groups. It is evident from an analysis of variance among these groups that differences do exist (Wilks' Lambda = 0.126, $F = 17.6^{**}$, df = 14,136).

The next step was to examine the nature of the differences among the groups. Those lake characters with the largest scaled vector values (calculated from the discriminant program) in Table 5 are the most important in differentiating among the lake groups. Since each group is defined along two discriminant axes, two scaled vector values are given for each character—one for each axis (I and II). In dimension I the order of decreasing importance of these characters is: $d$ (scaled vector $= 15.89$), transparency, alkalinity, pH, depth, conductivity, and area (scaled
TABLE 5. Analysis of variance of the 7 lake parameters that were used in separating the Danish lakes into three groups. Scaled vector values are obtained from the discriminant analysis program. Degrees of freedom: Within, 74; Among, 2

| Parameter               | Mean Square | F-ratio | Scaled Vectors |
|-------------------------|-------------|---------|----------------|
|                         | Within      | Among   |               |
| Transparency            | 405.5       | 14282.8 | 35.2**        | -11.67 | 4.85 |
| d                       | 26.8        | 908.3   | 37.5**        | -15.89 | -3.03 |
| Conductivity            | 46878.0     | 23343.0 | .5            | 2.45   | 3.62 |
| pH<sub>min</sub>        | 1.2         | 21.7    | 18.1**        | -4.20  | 1.45 |
| Alkalinity min.         | 8.8         | 15.5    | 18.5**        | -6.46  | -7.74 |
| Maximum depth           | 47.2        | 1022.5  | 21.7**        | -3.93  | 6.17 |
| Area                    | 294472.8    | 1097100.7 | 3.7**       | - .26  | .31 |

**=significant at p = 0.01

vector = 0.26). These values account for approximately 56% of the distinction made between lakes. The second scaled vector values (II) are ranked in a different order, with alkalinity, maximum depth, and transparency of primary importance (Table 5). This dimension of the discriminant analysis contributes the remaining 44% in defining the lake groups. A summation of the variables in the discriminant equation reduces the 7 parameters to two dimensions (I, II), and the points defined by the two discriminant scores can be plotted; this results in a clustering of points in three areas.

Each lake was then scored according to its discriminant value, and a probability was assigned to indicate which discriminant group it resembles most. Table 6 summarizes the p-values of the

TABLE 6. A summary of the results of the discriminant analysis on 77 Danish lakes, indicating how well the subjectively formed groups conform to the groups formed by the discriminant program (indicated from P values). Group 1 is the clear-water lakes, Group 2 the ponds and bogs, and Group 3 the polluted sites. A discussion in the text is included for those lakes not conforming to the 2 methods of grouping

| Assigned by Discriminant Grouping | 1  | 2  | 3  |
|-----------------------------------|----|----|----|
| Subjective                        | 26 | 2  | 1  |
| Classification                     | 3  | 21 | 0  |
| Lakes                              | 1  | 0  | 23 |

lakes for each group. In general a high degree of agreement is found between the lake group to which a lake was assigned subjectively and the probability of the lake occurring in that group according to the discriminant analysis. Of the clear-water lakes, Store Gribsø (29) and Ove Sø (53) have their greatest p-values in Group 2 (ponds and bogs), whereas Kalgaard Sø (40) has the highest p-value in the polluted lake group (Group 3). Both Store Gribsø and Ove Sø were placed in Group 2 because of the high importance of d and transparency (see scaled vector values, Table 5) in determining lake group and the low importance of area. Kalgaard Sø, on the other hand, is one of those lakes difficult to classify: its low conductivity and alkalinity suggest a non-polluted site, but the relatively high d value indicates high phytoplanktonic biomass (see Species Analysis for further discussion of d). Within the pond and bog group (Group 2) Geddesø (25), Hundsø (38), and Øjesø (77) had high probabilities in the clear-water group (Group 1). These lakes were probably put into Group 1 by the discriminant analysis because of their relatively high transparencies and the relatively low importance of area. Tuel Sø (74) was the only polluted lake with a high probability of belonging to another group (0.73, for clear-water lakes); a low d value from this site may have influenced this p value.

The advantage of a discriminant analysis will be discussed more fully in Species Grouping; however, it is obvious from the foregoing that it enables one to define lake groups objectively and to assign a particular body of water to its most appropriate lake group. In the present study the lake groups were defined on the basis of seven lake parameters, and the placement of any body of water in a group implies conformity within the range of the parameters (in toto) of that group. This step is a necessary prerequisite for any regional paleolimnological investigation. In essence it establishes a limnological frame of reference and attempts to remove some of the ambiguities associated with the use of more general terms.
Table 7. Correlation coefficients among the 22 most frequent species of chydorids and selected lake parameters.

| Species                   | Transpar. (%) | d         | Conduct. | pH_dHCO₃ | Alkalinit. (meq) |
|---------------------------|---------------|-----------|----------|----------|-----------------|
| Comptoceras rectirostris  | -0.9          | -0.58**   | -0.32    | -0.30    | -0.32*          |
| Aeroperus harpae          | -0.11         | -0.62**   | -0.51    | -0.56**  | -0.45**         |
| Alonopsis elongata        | -0.17         | -0.62**   | -0.30    | -0.45**  | -0.41**         |
| Chydorus lamellatus       | -0.31*        | -0.41**   | -0.30    | -0.34*   | -0.25           |
| Leydigia lepida           | -0.07         | -0.09     | -0.18    | -0.14    | -0.11           |
| Alona affinis             | -0.11         | 0.02      | -0.03    | -0.04    | -0.04           |
| A. quadranularis          | -0.25*        | -0.69     | -0.13    | 0.28*    | -0.001          |
| A. rostrata               | -0.25*        | -0.94**   | -0.03    | 0.04     | -0.20           |
| A. guttata                | -0.51*        | -0.27     | -0.07    | 0.23     | 0.04            |
| A. costata                | -0.16         | -0.24     | -0.04    | -0.24    | -0.16           |
| A. rustic             | -0.19         | -0.35     | -0.15    | -0.08    | -0.17           |
| Monopis dispar             | -0.19         | -0.10     | -0.18    | -0.31*   | -0.19           |
| Euryergus longistatus     | -0.35**       | -0.45**   | -0.29*   | -0.22    | -0.30*          |
| Alonella nana             | -0.18         | -0.55**   | -0.40*   | -0.40    | -0.30**         |
| A. eca           | -0.23         | -0.33*    | -0.56**  | -0.64**  | -0.30**         |
| A. exiguus              | -0.05         | -0.11     | -0.05    | -0.13    | -0.09           |
| Diaphorina reatra         | -0.10         | -0.41*    | -0.19    | -0.31    | -0.18           |
| Ephydorina walstonii      | -0.26         | -0.20     | -0.31    | -0.47*   | -0.28           |
| Chydorus sphaericus       | -0.13         | -0.41**   | -0.47**  | -0.61**  | -0.56**         |
| C. piper                | -0.46**       | -0.34*    | -0.37*   | -0.09    | -0.30**         |
| Pleuroxus trigonellas     | -0.17         | -0.11     | -0.19    | -0.39*   | -0.20           |
| P. uncinnatis            | -0.03         | -0.17     | -0.08    | -0.08    | -0.11           |

*Significant at p = 0.05
**Significant at p = 0.01

Species Analysis

Frey (1960) suggested a method with which a complete chydorid species list could be recovered from bottom sediments of a lake with a minimum of time and effort. By this method, a total of 35 species was recovered from the surficial sediments of Danish lakes, including three not previously reported from the country—Alona intermedia Sars, A. protzi Hartwig, and Chydorus latus Sars. The remaining 32 species have been previously reported by either Müller (1867), Poulsen (1928), or Berg (1929). Three species—Euryergus longistatus Lilljebørg, reported by Berg (1945) from a collection of Boisen Bennike, Chydorus gibbus Lilljebørg, reported by Berg (1929), and C. ovellis Kurz, reported by Poulsen (1928)—were not recovered from the surficial sediments, nor were they found in net samples collected during July 1965; nevertheless, a discussion of these species is included in the Species Analysis.

Commonly in species analyses attempts are made to associate certain species with particular lake parameters on a more or less subjective basis. Thus, it is not uncommon to find such statements that species are associated with low pH, or species are common at enriched sites. In order to quantify such statements, I have compared the abundance of the 22 most common species with selected lake characteristics (Table 7). Since the lake parameters in Table 7 are all interrelated (Tables 2–4), emphasis should not be placed on a single significant correlation, but overall information should be considered for each species. Spurious correlations that may occur can be eliminated by an evaluation of significant (or non-significant) correlations with related parameters. The following are interpretations of the possible meaning of significant correlations.

Transparency. In general the major factors affecting transparency in lakes are the presence or absence of suspended and dissolved materials. Low transparency in Danish waters indicates either bog-waters (or water stained with humic substances) in which transparencies are low due to specific water color, or highly productive waters in which the transparencies are influenced primarily by suspended materials and secondarily by dissolved substances. The best criterion for distinguishing between the two is the d value. Humic waters have low transparencies and correspondingly low d values (usually less than 10), whereas highly productive waters have low transparencies and high d values. Further distinctions among these lake types can be made by comparing conductivity, alkalinity, and pH values (Table 1); highly productive lakes generally have higher values for these parameters than humic-water lakes.

Any significant negative correlation of a species with transparency could indicate a preference (or tolerance) to those conditions found at enriched sites; a positive correlation suggests the inverse.

d. The signature d has been assigned to the increase of transparency after centrifugation of a water sample (see Methods), resulting from the removal of seston. It was obvious that the principal factor affecting d was the phytoplankton. Zooplankton, with its low abundance, had little or no effect on d, and the suspended inorganic material (tripton) had only a negligible effect. Hence, a reasonable assumption was to equate the d value to phytoplanktonic biomass. Because transparency measurements were based on the percent transmittance of light through a 10-cm cell, this assumption does not hold in cases where there are sufficient differences in the particle size to cause a differential scattering of light within the 10-cm cell.

Transparency and d values are highly correlated in the clear-water and polluted lakes (clear-water lakes, r = -0.49**; polluted lakes, r = -0.70**; ponds and bogs, r = 0.37 (Tables 2–4), as would be expected from the interpretation that d is primarily a measure of planktonic
Table 8. A summary of the distribution and relative abundance of the 22 most common chy dorid species found in Danish waters. The first column of average abundance is based on all lakes. Frequency data are number of occurrences of a species in lakes of a particular group divided by the total number of lakes in that group. Symbols: 1 = clear-water lakes, 2 = ponds and bogs, 3 = polluted lakes

| Species                | Total No. Ocur. | Relative average abundance (%) | Frequency |
|------------------------|-----------------|--------------------------------|-----------|
|                        |                 | All Lakes                     | Lake Group | All Lakes                     | Lake Group |
|                        |                 |                               | 1   2   3 |                               | 1   2   3 |
| Chydrorus sphaericus   | 77              | 38.5                          | 30.0 19.0 60.5 | 1.00                      | 1.00 1.00 1.00 |
| Alona affinis          | 71              | 7.5                           | 9.0   5.5 7.0 | 0.92                      | 0.97 0.91 0.88 |
| Alona quadriangularis  | 70              | 10.0                          | 13.0  6.5 9.0 | 0.91                      | 0.90 0.83 1.00 |
| Alona rectangularis    | 68              | 7.0                           | 5.0   5.0 14.0 | 0.88                      | 0.83 0.88 0.96 |
| Aeroperus harpa     | 65              | 6.0                           | 5.0   10.5 15.5 | 0.84                      | 0.97 0.96 0.88 |
| Alonella nanana       | 58              | 9.0                           | 6.0   16.0 1.0 | 0.75                      | 0.72 1.00 0.54 |
| Eury cercus lamelatus  | 57              | 4.0                           | 4.0   5.0 1.0 | 0.74                      | 0.90 0.79 0.50 |
| Pleurozus uncinitus   | 56              | 3.5                           | 4.0   3.0 3.0 | 0.73                      | 0.79 0.46 0.92 |
| Campleocercus rectirostris | 55           | 4.0                           | 4.0   5.0 1.0 | 0.71                      | 0.76 0.75 0.63 |
| Grapho loberis testudinaria | 53          | 4.0                           | 3.0   6.5 0.5 | 0.69                      | 0.72 0.96 0.38 |
| Monosiphus dispar     | 46              | 3.0                           | 3.5   3.0 3.0 | 0.60                      | 0.86 0.54 0.33 |
| Leydigi leydigi       | 45              | 3.0                           | 3.0   6.0 2.5 | 0.58                      | 0.66 0.47 0.92 |
| Chy drorus piger      | 40              | 2.5                           | 4.0   2.0 1.0 | 0.52                      | 0.69 0.88 0.25 |
| Alonopa elonga       | 38              | 3.0                           | 3.0   4.5 0.5 | 0.49                      | 0.76 0.57 0.25 |
| Alonella eximia       | 37              | 7.5                           | 3.5   11.0 0.0 | 0.48                      | 0.62 0.79 0.00 |
| Dis paralona rostrata | 36              | 1.5                           | 2.0   1.5 1.0 | 0.47                      | 0.41 0.50 0.50 |
| Rhy nchocer alafalcata | 28           | 4.0                           | 3.0   7.0 1.5 | 0.36                      | 0.55 0.38 0.13 |
| Alona guttata        | 23              | 1.5                           | 3.0   1.0 0.5 | 0.30                      | 0.21 0.50 0.21 |
| Pleurozus trigonalis  | 22              | 1.5                           | 1.0   2.0 1.0 | 0.28                      | 0.28 0.38 0.21 |
| Alona rustica        | 19              | 3.0                           | 3.5   3.0 1.0 | 0.24                      | 0.24 0.41 0.08 |
| Alonella exigua       | 19              | 2.5                           | 2.0   2.5 1.0 | 0.24                      | 0.31 0.38 0.04 |
| Alona costata        | 19              | 1.0                           | 1.0   1.5 1.0 | 0.24                      | 0.38 0.20 0.13 |

Biomass. An assessment of the d and transparency values is useful in establishing which lakes are highly polluted (see Lake Groupings). A positive correlation of a chy dorid species with d implies that the species thrives at enriched sites.

Conductivity. Conductivity is directly related to several water characteristics, most important of which is salinity. Except for Flade Sø (16), which is adjacent to the North Sea, the Danish lakes are not unusual in their alkaline-earth components, so that calcium content is most important in determining conductivity values. In the three groups of Danish lakes, high conductivity is consistently associated with high alkalinity, and low conductivity with low alkalinity (Tables 2–4). Any significant positive correlation of a species with conductivity suggests a tolerance of saline conditions; however, the total range of conductivity is not extremely high, and therefore such correlations have limited biological information. On the other hand, many of the Danish lakes have fairly low conductivities. A significant negative correlation of a species with conductivity suggests that the species prefers certain conditions associated with sites having low conductivities, i.e., low alkalinitities.

pH and Alkalinity. Alkalinitities in the Danish lakes are closely associated with the activity of calcium carbonate. In regions where calcium content of the soils is high, the alkalinity of the lakes will be high. The principal factor affecting pH changes in lakes is the amount of calcium carbonate available to buffer the effects of intense photosynthesis, and a close relationship among these parameters exists. Mininum pH and minimum alkalinity values were selected to compare lakes and species. Low pH values generally occur in bog waters and in those clear-water lakes with low alkalinitities. Within these two groups there is a close relationship between pH and alkalinity (Tables 2 and 3). The lack of a significant correlation in the polluted lakes has probably resulted from biological decalcification (Table 4).

The pH and alkalinity data in Table 1 have been assembled from many sources, yet they display trends. The problem is in deciding how closely these values relate to the littoral and benthic habitats of the chy dorids. A significant positive correlation between a species and these measurements suggests a preference for more basic conditions, while a significant negative correlation suggests that the species prefers acid lake conditions.

The total number of significant correlations in Table 7 is interesting. Transparency has 4 positive and 2 negative correlations; conductivity has 7 negative correlations and 1 positive correlation; d has 9 negative and 2 positive corre-
Table 9. A summary of the frequency and "preference" of 13 species of chyadorids infrequently found in Danish waters. "Preference" is the number of occurrences of a species in a lake group divided by the total number of occurrences of the species. Symbols are the same as Table 6.

| Species            | Total No. Occur. | All Lakes | Frequency | "Preference" |
|--------------------|------------------|-----------|-----------|--------------|
|                    |                  |           | Lake Group| Lake Group   |
|                    |                  |           | 1         | 2         | 3         | 1         | 2         | 3         |
| Percantha truncata | 10               | .13       | .07       | .25       | .08       | .20       | .60       | .20       |
| Alona intermedia  | 9                | .11       | .14       | .21       | .00       | .45       | .55       | .00       |
| Pseudochyadorus globosus | 9     | .11       | .03       | .25       | .08       | .11       | .67       | .22       |
| Aeroperus angulatus | 7               | .09       | .07       | .04       | .17       | .29       | .14       | .57       |
| Pleuroxus laevis  | 7                | .09       | .03       | .21       | .04       | .14       | .72       | .14       |
| Leydigia acanthocercoides | 6     | .08       | .00       | .00       | .25       | .00       | .00       | 1.00      |
| Camptocercus lilljeborgii | 5    | .06       | .07       | .13       | .00       | .40       | .60       | .00       |
| Pleuroxus adenues | 2                | .02       | .03       | .04       | .00       | .50       | .50       | .00       |
| Anchistropus emarginatus | 1    | .01       | .03       | .00       | .00       | 1.00      | .00       | .00       |
| Oxyella tenuicauda | 1                | .01       | .00       | .04       | .00       | .00       | 1.00      | .00       |
| Kurzia latissima   | 1                | .01       | .00       | .04       | .00       | .00       | 1.00      | .00       |
| Alona protzi      | 1                | .01       | .03       | .00       | .00       | 1.00      | .00       | .00       |
| Chyadorus latus   | 1                | .01       | .00       | .04       | .00       | .00       | 1.00      | .00       |

Acidic conditions; pH has 8 negative and 2 positive correlations; alkalinity has 7 negative correlations and 1 positive correlation. The biological meaning suggested by these negative correlations is that the chyadorids, as a group, are most closely associated with oligotrophic-type lakes of low productivity. This would also include bog-type lakes, since many species occur in these localities (see section on Species Diversity). The exceptions to this general statement will be discussed as each species is considered.

An attempt has also been made to give a quantitative insight into the distribution of the individual species in relation to lake types. For each species that occurred in at least 19 of the lakes sampled the average relative abundance was calculated for clear-water lakes, polluted clear-water lakes, ponds and bogs, and all lakes combined (Table 8). Alona quadrangularis has an average relative abundance in clear-water locations almost twice as great as in any other lake group.

A second calculation is frequency, which is the number of occurrences of a species in a particular group of lakes divided by the total number of lakes in that group. Frequency is not necessarily related to average abundance, as it indicates the distribution of a species among lakes of a particular type. A species can be more abundant within one lake group, but still occur with a higher frequency within another group. For example, Alona quadrangularis has its highest average abundance (13.0%) in clear-water lakes yet occurs with a higher frequency (1.00) in polluted lakes. Such a species is regarded as being most abundant in clear-water lakes but also as being tolerant of polluted conditions.

The 35 species of chyadorids recovered were not distributed uniformly in the Danish lakes. Table 9 shows that 13 species occur in fewer than 10 of the lakes. It would be meaningless to calculate the relative average abundance of these species because of their low abundance; therefore, only frequency and preference values have been calculated. A preference value is the number of occurrences of a species in a group of lakes divided by the total number of occurrences of that species. Species with fewer than 5 occurrences probably cannot be interpreted reliably by any measure, so that frequency and preference in these instances merely indicate the types of localities from which the species have been recovered.

For any given species the highest relative abundance is assumed to indicate the group of lakes in which conditions are most favorable for the species. Sometimes an unusually high percentage of a species in one lake may affect the average relative abundance value for that group of lakes. Such high percentages will be pointed out in the discussion of the individual species. Frequency values are not interpreted as being indicative of the favorability of a habitat for a species, but as a measure of the species' ubiquity.

Because the abundance and frequency data of chyadorid species in the Danish lakes are based on remains recovered from the surficial sediments and not on spot samples taken with nets, the data in Tables 7, 8, and 9 represent a quantified, reasonably accurate summary of the ecological affinities of the species.
Camptocerus rectirostris Schödler was reported from Denmark by Müller (1867), Poulsen (1928), Berg (1929), and Berg and Petersen (1956). Frey (1962) found remains of this species from the Eemian interglacial. Berg (1929) commented that C. rectirostris is common in large ponds and the near-shore areas of lakes. Poulsen (1928) placed this animal in his pH group I (3.8–6.0).

In the present study this species was recovered from 55 lakes. Significant negative correlations with $d$, conductivity, pH, and alkalinity (Table 7) suggest that C. rectirostris would be found in non-polluted lakes of low productivity. The greatest average abundance of this species is in the group of ponds and bogs, while its largest frequency value is in the clear-water group (Table 8). The low values for abundance and frequency at the enriched sites suggest this species is most abundant in ponds and bogs but is frequent in most Danish waters that are not culturally affected. Berg (1929) collected this species from Glenstrup Sø (26), but no sedimentary remains were recovered from this site. Poulsen’s (1928) contention that C. rectirostris is most common in waters of low pH is probably correct.

Camptocerus lilljeborgi Schödler was reported from Denmark previously by Müller (1867), by Poulsen (1928, who claimed it was associated with alkaline waters), and by Berg (1929, who noted it in the same type of habitat as C. rectirostris—fairly large ponds and near-shore areas of lakes—but with lower frequency). In the present study it was recovered from only 5 lakes, with the most frequent occurrence at pond and bog sites (Table 9). Although Berg (1929) collected this species at Bondedam (6) and Løgsgård (17), no remains were recovered from these localities. Its highest preference (Table 9) was pond and bog localities (.60), which is in disagreement with the conclusions of Poulsen (1928) that it occurs mainly in alkaline waters.

Acroperus harpae Baird has been found by numerous investigators in Denmark (Müller, 1867; Poulsen, 1928; Berg, 1929, 1948; Røen, 1954; and Frey, 1962). Berg (1929) stated that this species occurs in puddles, peatbogs, small and large ponds, and in the littoral of lakes; he suggested its preferred habitat is the littoral zone. Poulsen (1928) put A. harpae into pH group III (7.1–7.9) but reported that it is fairly abundant in all groups. Berg (1948) reported this species from the littoral vegetation along the Susaa River and also in the “mud fauna” from this river. In the present study it was found in 65 lakes. Judging from its significant negative correlations with $d$, conductivity, pH, and alkalinity (Table 7), this species should be most common in low-productivity lakes, ponds, and bogs. It is evident from data in Table 8 that A. harpae is most common in ponds and bogs and secondarily in clear-water lakes; its abundance and frequency are notably low in the polluted lake group. A. harpae is a common component of the Danish chydorid fauna, present at many sites, but it occurs most abundantly at those localities characterized by low productivity, pH, conductivity, and alkalinity.

Acroperus angustatus Sars was first reported from Denmark by Müller (1867) and then by Berg (1929), Fig. 7, Plate III). It was recovered from the sediments of 7 lakes, among which it exhibited both highest frequency and preference in polluted lakes, which suggests that this species is found most often at enriched localities.

Alonopsis elongata Sars has been reported from Denmark by Müller (1867), Poulsen (1928), Berg (1929), Røen (1954), Berg and Petersen (1956), and Frey (1962). Berg (1929) reports it not rare but infrequent in the littoral of lakes. Poulsen (1928) states that it is found mostly in pH group II (6.1–7.0), but that it ranged from pH groups I–III. It was found at 38 localities in the present study. This species has highly significant negative correlations with $d$, pH, and alkalinity, which suggest that it lives in non-polluted, fairly oligotrophic lakes or in ponds and bogs. Its average abundance is highest in the pond-and-bog type, while its most frequent occurrence is in the clear-water sites. It has low abundances and frequencies at polluted localities. One may conclude that A. elongata is most abundant in ponds and bogs but that it also occurs with a high frequency (but not so abundant) in clear-water lakes.

Kursia latissima (Kurz) was represented by the recovery of 3 head shells from Hjortesøle (35). Previously this species was reported by Berg (1929) from Koberdam (44) and Gadevåg Nørgård (24), even though no sedimentary remains were recovered from these localities in the present study. Berg states that K. latissima is rather rare, and, on the basis of its presence at only pond and bog sites, it should be considered confined primarily to these localities.

Graptoleberis testudinaria (Fischer), found at 53 localities in the present study, was considered by Berg (1929) to be a common species of the bottom fauna in littoral areas, although Frey (1968) presents convincing arguments for its specialization to a vegetational habitat. Poulsen (1928)
puts it with the lowest pH group. It was also reported by Berg (1948), Røen (1954), and Frey (1962) from Denmark. *G. testudinaria* was most abundant and most frequent in ponds and bogs (Table 8), and although it does occur at enriched sites, its average abundance at these localities was very low (.5%). The highly significant negative correlation of this species with *d*, and significant negative correlations with conductivity and pH support these conclusions (Table 7). The significant negative correlation between *G. testudinaria* and transparency suggests that the abundance of this species decreases as non-tripton-controlled transparency increases. This correlation reflects the high abundance of this species in bog waters.

*Leydigia leydigi* (Schödler) was previously reported from Denmark by Müller (1867, *Alona leydigi*), Berg (1929, 1948), Frey (1962), and Johnsen *et al.* (1962). Berg (1929) stated that *L. leydigi* is a pronounced bottom form. Its greatest average abundance was in ponds and bogs, but it was most frequent in polluted lakes. One may conclude that the most favorable conditions for this species occur in ponds and bogs, but because it is a bottom dweller it may be frequent at polluted localities.

*Leydigia acanthocercoides* (Fischer) was reported from Denmark by Müller (1867, *Alona acanthocercoides*, Table IV, Fig. 5), and by Frey (1962). This species was found in the present study in only 6 lakes, with a high frequency and a high preference value at polluted sites. Since *L. acanthocercoides* was never abundant, one concludes that it is a rare species found primarily at polluted localities.

*Oxyurella tenuicaudis* (Sars) was reported from Denmark by Müller (1867), Poulsen (1928), and Berg (1929, 1948). Poulsen (1928) does not put this species into any of his pH groups, and Berg (1929) stated that *O. tenuicaudis* was rare in bog-holes and ponds with abundant vegetation. Only one specimen, represented by a post-abdomen, was found at the pond of Gødevang Nøglesø (24). Berg (1929) found this species at nearly Gedevang bog and also at Hulsø (37) and Sortedam (65), which are considered ponds. Hence this species is rare in Denmark and found mainly in ponds.

*Alona affinis* (Leydig) was one of the most common and frequent species in Denmark, having been recovered from the sediments of 71 lakes. This species resembles closely *Alona oblonga* of Müller (1867, Table III, Fig. 22 and 23, and Table IV, Fig. 1 and 2; Fig. 2 is a diagram of the head pores of *A. affinis*). It has been reported from Denmark by Poulsen (1928), who placed it in his pH group III (7.1–7.9), and by Berg (1929, 1948). Frey (1962) recovered it from interglacial sediments. *A. affinis* has no significant correlations with any of the lake parameters studied (Table 7), and, although most abundant and frequent at the clear-water sites, it is fairly evenly distributed in abundance and frequency among the three lake groups (Table 8). *A. affinis* is a cosmopolitan species inhabiting the bottom muds of lakes (Fryer, 1968).

*Alona quadrangularis* (Müller) has been reported from Denmark by numerous authors (Müller, 1867; Poulsen, 1928; Berg, 1929, 1948; Røen, 1954; Johnson *et al.*, 1962; Frey, 1962). As with *A. affinis*, this species is common in Denmark, occurring in 70 lakes. Its distribution and abundance (Table 8) was very similar to that of *A. affinis*, except that it may have a tendency to occur more often in polluted lakes. The positive correlations with transparency and alkalinity in Table 7 are not meaningful, because no logical biological argument can be made to interpret these variables when the other interrelated parameters are not correlated. This species inhabits the bottom muds of lakes.

*Alona intermedia* Sars had not been previously reported from Denmark. Berg (1929) stated that this species probably does occur, although he did not find it in his collections. *A. intermedia* was found in the sediments of 9 lakes. It was most frequent in ponds and bogs, and it also had its highest preference value at these sites (Table 9). The species was also present at clear-water sites but absent from polluted localities. It would appear that from these data *A. intermedia* is confined to unpolluted lakes.

*Alona rectangula* Sars was first reported from Denmark by Poulsen (1928) and has since been reported by Berg (1929, 1948) and Frey (1962). It was present in 68 lakes, with its most abundant percentages and highest frequency at polluted sites (Table 8). This species, like *C. sphaericus*, occurs in the limnetic area of polluted lakes. The abundance of *A. rectangula* is not so great as *C. sphaericus* in the most polluted sites, but it is so in lakes that are either recovering from pollutional effects or are mildly polluted.

*Alona guttata* Sars occurs in 23 of the lakes studied. Berg (1929) stated that it was first identified from Denmark by a single specimen taken from Furesø (20) by Wesenberg-Lund (in Wesenberg-Lund *et al.*, 1917); earlier reports of this species by Müller (1867) were apparently in
error. It was also reported present in Danish lakes by Poulsen (1928), Berg (1948), and Frey (1962). The greatest average abundance of *A. guttata* was in the clear-water lakes, and it was most frequent in ponds and bogs (Table 8). The greater average abundance of this species at clear-water sites was due to its relatively high abundance at two clear-water lakes—Almindø (1), and, Thorsø (71)—where percentages were 4.1 and 5.1, respectively. *A. guttata* probably is found mainly in ponds and bogs, and since it is positively correlated with transparency it is most common in ponds (i.e., species abundance increases with transparency, whereas if it were more abundant at bogs the species abundance would be negatively correlated with transparency).

*Alona costata* Sars has been reported from Denmark by Poulsen (1928) and Berg (1929, 1948). Berg (1929) stated that it was a common littoral form of lakes and large ponds; Poulsen (1928) placed it in his pH group III (7.1–7.9). This species was found in 19 lakes in the present study. Its greatest average abundance was in ponds and bogs, and its greatest frequency was at clear-water sites (Table 8). *Alona costata* is not too frequent in Danish lakes (.24, overall), and where it does occur it is usually a minor component of the chydrid association. It is found most frequently in clear-water localities.

*Alona rustica* Scott was first reported from Denmark by Frey (1965). Being very similar in its morphology to *A. costata*, it was probably confused with this species in Denmark prior to 1965. *A. rustica* was found in 19 lakes, with its greatest average abundance in clear-water sites. Its greatest frequency was at ponds and bogs (Table 8). This species had an overall average abundance of 3.0%, but it was quite abundant at Groversø (30: 9.9%), Madum So (48: 6.2%), and Grane Langsø (27: 6.1%). Although there are no significant correlations of this species with the lake parameters (Table 7), it is evident from the high relative abundance at the above three lakes that the species is most abundant at low alkalinitities (Table 1).

*Alona protsi* Hartwig had not previously been reported from Denmark. One shell from the surficial sediments of Slaensø (63) was typical of this species with two small teeth at the post-ventral corner of the shell. *A. protsi* is rare, and no ecological inferences can be drawn from the very limited data of this study.

*Monosphius dispar* Sars, according to Berg (1929), was first reported by Müller (1867) from a collection made by Lund at Farum Sø (14). This species has been collected by Poulsen (1928), Berg and Petersen (1956), Røsen (1954), and Frey (1962). According to Berg (1929), it is found chiefly in collections from muddy bottoms and restricted to lakes or very large ponds. The greatest abundance of *M. dispar* was at Store Øksø (80: 20.5%) and Flynderø (17: 17.0%). It was present in almost equal abundance in all three lake groups and was most frequent at clear-water sites (Table 8).

*Eury cercus lamellatus* (Müller) is a very common chydrid in Denmark. It was first reported by Müller (1867) and has since been found by Poulsen (1928), Berg (1929, 1948), Røsen (1954), and Frey (1962). Berg (1929) reported that it was frequent and often present in large numbers, although not generally found in impermanent puddles, small ponds, and peat bogs. Poulsen (1928) concluded that this species was fairly well distributed over pH ranges. In the present survey, it occurred in 57 lakes, with the largest average abundance in ponds and bogs. It was most frequent at clear-water sites, where its average abundance almost matched that of the ponds and bogs (Table 8). It was positively correlated with transparency and negatively correlated with *d*, conductivity, and alkalinity. It is evident that this species prefers non-polluted localities.

*Alonella nana* (Baird) has been found in Denmark by Poulsen (1928), Berg (1929, 1948), Berg and Petersen (1956), and Frey (1962). It is a fairly common species, occurring in 58 lakes. It is quite obvious that *A. nana* is rare at polluted sites (Table 8), as its average abundance at these localities was far below its overall average abundance. It was most frequent and most abundant at pond and bog lakes. The highly significant negative correlations with all parameters except transparency (Table 7) suggest that this species is found in oligotrophic-type sites. Poulsen (1928) placed this species in pH group II (6.1–7.0). It is evident from the data in Tables 7 and 8 that this animal is most abundant in ponds and bogs and waters of low productivity.

*Alonella excisa* (Fischer) is less common than *A. nana* (occurring in only 37 lakes), but its ecological preference for habitat seems quite similar. With the exception that it is completely absent from polluted sites, this species has an almost identical relationship as *A. nana* (Tables 7 and 8). Poulsen (1928) included this species in pH group I (3.8–6.0), and Berg (1929) found it fairly common in the littoral of lakes and ponds. *A. excisa* was also mentioned in papers by Berg
(1948), Berg and Petersen (1956), and Frey (1962).

Alonella exigua (Lilljeborg) was reported previously by Poulsen (1928), Berg (1929, 1948), and Frey (1962). Müller (1967) reported this species as Pleuroxus exigus (Table IV, Fig. 16 and 17). Among the 19 lakes from which it was recovered, it was most frequent in clear-water lakes and in ponds and bogs. A. exigua was never very abundant, with an average abundance of 2.5%, and a maximum abundance of 7.9% in Fjøstrup Sø (22). There are no significant correlations of this species with any measured lake parameter (Table 7), but from its average abundance and frequency (Table 8) it appears to be similar in habitat requirements to A. nana and A. excisa in that it is not normally found at polluted sites.

Dispharalona rostrata (Koch) (formerly Alonella rostrata—See Fryer 1968) was found by Müller (1867, Alona rostrata), Poulsen (1928), Berg (1929, 1948), and Frey (1962). It is fairly common and is most likely a bottom dweller, as are some of the other chydorids. D. rostrata was most abundant in Thorsø (7.0%), but generally it was present in the surficial sediments in low relative abundances. The average abundance and frequency values varied little among the three lake groups, so it must be primarily a bottom dweller unaffected by vegetational differences that might exist among these lake groups. The one significant negative correlation with d (Table 7) seems spurious, as there are no other interrelated correlations.

Rhynchotalona falcata (Sars) was reported by Müller (1867) as Alona dentata (Table IV, Figs. 6, 7) and A. falcata; both of these named species are probably what we now call R. falcata. Poulsen (1928), Berg (1929), and Øren (1954) have also reported this species. Berg (1929) stated that this species was rare, and Poulsen (1928) placed it in his pH group III (7.1–7.9). It was found in 28 lakes, with most of the animals recovered from ponds and bogs. R. falcata has an average abundance of 4.0% (Table 8), but this was influenced by high percentages at Store Øksø (80: 34.9%), Madum Sø (48: 14.6%), Mossø (50: 11.4%), and Store Gribsø (29: 10.9%). This species was rare in polluted lakes. A significant negative correlation of R. falcata with pH suggests that this species prefers more acidic sites but is most abundant in ponds and bogs.

Chydorus sphaericus Müller is undoubtedly the most cosmopolitan species of the Chydoridae. It has been reported by numerous investigators from Denmark, including Müller (1867), Wesenberg-Lund (1904), Poulsen (1928), Berg (1929, 1948), Berg and Nygaard (1929), Krogh and Berg (1931), Øren (1954), Frey (1962), and Johnson et al. (1962). This species was found in all lakes sampled. It was most abundant in highly polluted lakes [90.9% in Pedersborg Sø (54)], and least abundant in the other two lake groups [0.6% at Store Gribsø (29) and 2.2% at Filøs (15)]. Due to its relatively high percentages in many lakes, C. sphaericus had the highest overall average abundance of all species (Table 8). It is most abundant at polluted sites (60.5%), and, unlike most chyadorid species, the correlations in Table 7 are nearly all positive and highly significant. This supports the idea that this species is most common at enriched sites.

Chydorus piger Sars has been previously reported by Poulsen (1928) and Frey (1962). It was found in 40 lakes, with its greatest abundance in clear-water lakes and secondarily in ponds and bogs (Table 8). C. piger was most frequent in clear-water lakes, and the significant correlations with transparency, conductivity, and alkalinity (Table 7) suggest that this species is best suited for non-polluted, clear-water sites. Its greatest abundance was 12.3% at the Jutlandic lake of Snabe-Igelsø (64). Fryer (1968) believes this species is best adapted for benthic existence.

Chydorus latus Sars had not previously been reported from Denmark. It was represented by three shells and three post-abdomens from the bog of Lille Øksø (79). Frey collected this species in July and August 1963 from two sites—Mørkesø, which is a bog near Silkeborg in Jutland, and Lille Gribsø (28), a bog lake in Zealand. From these reports it appears that C. latus is most frequent at bog sites, and it may be restricted to such waters.

Pseudochyodus globosus Baird (formerly Chydorus globosus—See Fryer, 1968), although reported by Berg (1929) to occur sometimes in considerable numbers, was relatively low in abundance (Table 8), never exceeding 3.0% in any lake. It had previously been reported from Denmark by Müller (1867), Poulsen (1928), Berg and Peterson (1956), and Frey (1962). P. globosus is a scavenger (Fryer, 1968) and is capable of surviving at all sites. It seems to have a preference for ponds and bogs, and of the 9 occurrences in Denmark 6 were at ponds and bogs (Table 9). This species was not found in Esrom Sø (13), Store Gribsø (29), Silkeborg Langsø
Pleuroxus uncinalis Baird is the most common Pleuroxus species recovered, occurring in 56 lakes. It has been found by Müller (1867, P. personatus, Table III, Fig. 26 and Table IV, Figs. 21–23), Poulsen (1928), Berg (1929, 1948), and Frey (1962) in Denmark. The average abundance of this animal was not greatly different for any lake group, but it was most frequently found in culturally affected lakes. The low frequency value in ponds and bogs suggest this species may prefer muddy bottoms, as postulated by Berg (1929). It has no significant correlations in Table 7.

Tretoccephala ambigua (Lilljeborg) was reported by Berg (1929, Alonopsis ambiguа) from Sorte Dam (65). No exuviae were recovered from any of the lakes studied, but abundant live material was collected in October 1966 from the channel between Parum Sø (14) and Furesø (19), where Frey (1965b) had collected it previously. This species is probably most abundant in shallow, eutrophic-type situations.

The following three species were not found in the surficial sediments but have been found in Denmark:

Eury cercus glacialis Lilljeborg was first reported from Denmark by Berg (1945) from collections made by Boisen Bennike. Kaiser (1959) published information regarding some ecological aspects of this species. It has been found only in small, impermanent lakes in the vicinity of Thy in Jutland. Kaiser considered E. glacialis an infrequent species, confined mainly to acidic oligotrophic-type lakes. No specimens were recovered from surficial sediments of the Thy lakes or from net samples.

Chydorus gibbus Lilljeborg was reported from Denmark by Berg (1929), who stated, “only one specimen of C. gibbus has been found in a mire sample from the shore of Sorte Sø on the estate of Holstenshuis (Isle of Funen), 28/10 26. The species has not previously been observed in this country.” This species must be very rare in Denmark, for, although no Funen lakes were sampled, no specimens were recovered in any of the 80 lakes sampled.

Chydorus ovalis Kurz was not recovered from the surficial sediments. Poulsen (1928) found it among the sparse vegetation of a north Jutland lake in the Thy region, while Røen (1954) reported this species from Grane Langsø (27). It is likely that C. ovalis is present in many of the lakes studied; however, the methods employed to
Table 10. Analysis of variance of 22 chydorid species for significant differences among the three groups of Danish lakes. Scaled vector values, obtained from the discriminant analysis, indicate the importance of each species in defining the lake groups by species. See text for further explanation.

| Species                        | Mean Square Within | Mean Square Among | F-ratio  | Scaled Vectors I | Scaled Vectors II |
|-------------------------------|--------------------|------------------|----------|-----------------|------------------|
| Eury cercus lamellatus         | 0.0878             | 0.135            | 15.4**   | .16             | -13              |
| Camplocerus retirostris       | 0.0210             | 0.080            | 6.1**    | .25             | -15              |
| Acroperus harpa               | 0.0202             | 0.320            | 26.7**   | .10             | -13              |
| Graptoleberis testudinaria    | 0.00756            | 0.235            | 31.1**   | .35             | .21              |
| Alona affinis                 | 0.01729            | 0.045            | 2.6      | .01             | .14              |
| A. quadrandulans              | 0.02283            | 0.110            | 4.8      | .22             | -17              |
| A. rectangula                 | 0.02229            | 0.100            | 5.9      | -.01            | .26              |
| A. guttata                    | 0.00283            | 0.005            | 1.8      | .13             | .01              |
| A. coastata                   | 0.00243            | 0.000            | 0.0      | .02             | -0.07            |
| A. rustica                    | 0.00527            | 0.020            | 3.4      | .02             | .01              |
| Leydigia leydigii             | 0.00984            | 0.045            | 5.2      | .06             | .17              |
| Alonella nana                 | 0.01440            | 0.755            | 47.7**   | .47             | .14              |
| A. ex sizes                   | 0.01797            | 3.55             | 19.8**   | .04             | -3.1             |
| A. exigua                     | 0.00432            | 0.015            | 3.5      | -.17            | -2.7             |
| Disparalona rostrata          | 0.00432            | 0.005            | 1.2      | .03             | -.03             |
| Pleuroxus trigonellus         | 0.00297            | 0.005            | 1.7      | .03             | .02              |
| P. uncinatus                  | 0.00632            | 0.025            | 2.7      | .12             | -1.0             |
| Chydorus sphaericus           | 0.07891            | 1.360            | 17.2**   | .26             | .17              |
| C. piger                      | 0.00716            | 0.005            | 9.1**    | -.16            | -10              |
| Monospilus dispar             | 0.00886            | 0.080            | 8.1**    | -.25            | -34              |
| Alonopis elongata             | 0.00743            | 0.075            | 10.1**   | .04             | .15              |
| Rhynchotalona falca           | 0.01202            | 0.040            | 3.3      | .27             | .37              |

**Significant at p = 0.05.
*Significant at p = 0.01.

retrieve the chydorid remains do not retain the smaller parts of these animals. Since the distinctive and characteristic olfactory setae of C. ovalis are found on the antennules, these animals may have been overlooked and their shells and head shields identified as C. sphaericus.

SPECIES GROUPINGS

The 77 Danish lakes were subjectively grouped into three categories on the basis of 7 characteristics. The results of the multiple discriminant analysis performed on these groupings were in close agreement with the initial subjective classifications, and those lakes not conforming to the initial groupings have been discussed. This statistical appraisal of the validity of the classification groups was necessary before the species can be grouped on the basis of the same lake categories.

The relative abundances of the 22 most common species (Table 8) were used as variables in the multiple discriminant analysis of the clear-water lakes, ponds and bogs, and polluted sites (Groups 1, 2, and 3). The advantages of using discriminant analysis, which emphasizes the differences in species composition between lake groups, are analogous to those in forming lake groups, i.e., 1) the multivariate null hypothesis that the means of the 3 lake groups are the same for all 22 chydorid species was tested, 2) individual F-ratios were calculated for each species, 3) scaled vector values were assigned to each species, 4) group centroids were calculated and plotted, and 5) probability values were assigned to species associations from each lake based on its discriminant score. Because the data were in the form of relative percentages (proportions), an arcsine transformation was performed on the raw data prior to discriminant analysis. This procedure produces an approximately constant variance within each variable (species).

There were no reasons a priori for anticipating that differences might exist among the chydorid associations of the 3 lake groups, but with the data available from Table 8 one might suspect differences between polluted and non-polluted sites. Likewise, there was no reason to expect differences between the clear-water lakes and the ponds and bogs, but the results of the analysis of variance between groups indicate differences do exist (Wilks' Lambda = 0.111, F = 4.84**, df = 44, 106). Table 10 summarizes the analysis of variance between species and gives the scaled vector values of the two discriminant axes. According to the scaled vector values of discriminant I, the following species are considered important indicators of lake types: Alonella nana (0.47), Graptoleberis testudinaria (0.35), Rhynchotalona falca (.27), Chydors sphaericus (0.26), Camp-
tocercus rectirostris (−0.25), Monosoplus dispar (−0.25), and Alona quadrangularis (0.22).

The rankings of discriminant II are somewhat different, with Alonella excisa (−0.31), Alonella exigua (−0.27), and Alona rectangula (0.26) assuming some importance on this axis. It is evident if one plots the centroids for each group that the scaled vectors along discriminant I are more important in distinguishing Group 2 from Groups 1 and 3, i.e., there is not a large difference in discriminant I values between I and 3, but there is between 1 and 3 versus 2 (Centroids: Group 1, I = 21.9, II = −4.3; Group 2, I = 37.7, II = 3.9; Group 3, I = 16.5, II = 8.6). The scaled vectors along discriminant score II show differences among all three groups.

The transformed means (Table 11) of the species abundance of the three lake groups suggest the following relationships among the more “important” chydrorid species:

**Camptocercus rectirostris**—Highest percentages in clear-water lakes, followed closely by ponds and bogs.

**Graptocercus testudinaria**—Highest percentages in ponds and bogs, lowest in polluted lakes.

**Alona quadrangularis**—Highest percentages in clear-water lakes, followed by polluted sites.

**Alona rectangula**—Most abundant at polluted sites, followed by ponds and bogs, and clear-water lakes.

**Alonella nana**—Highest percentages in ponds and bogs, lowest in polluted lakes.

**Alonella excisa**—Highest percentages in ponds and bogs, absent from polluted sites.

**Alonella exigua**—Almost equally abundant in clear-water lakes and ponds and bogs, but slightly higher percentages in the latter; almost absent from polluted sites.

| Species Groupings Assigned by Discriminant Analysis | 1 | 2 | 3 |
|-----------------------------------------------------|---|---|---|
| Discriminant classification of lakes                | 1 | 2 | 3 |
| Chydorus sphaericus—Highest percentages in polluted lakes, followed by clear-water sites; lowest in ponds and bogs. | 23 | 22 | 0 |
| Monosoplus dispar—Highest percentages in clear-water lakes; lowest in polluted sites. | 0 | 5 | 19 |
| Rhychotakina falcata—Evenly distributed in clear-water lakes and ponds and bogs; lowest percentages in polluted lakes. | 0 | 5 | 19 |

The relationships suggested by these means are not greatly different from those outlined previously (Species Analysis, and Table 8).

The differences between the probability of a lake belonging to a particular lake group (based on relative species abundance) and the lake groups previously defined (Lake Groupings) are summarized in Table 12. Clear-water lakes (Group 1) with high probabilities of belonging to Group 2 (ponds and bogs) were Store Grib (29) and Kuls (40), while four Group 1 lakes were classified as polluted (Group 3) on the bases of their species composition. Although the p values were very close between Groups 1 and 2 (0.42 vs 0.58), Kuls was placed in Group 2 due to a high discriminant I score, since this score placed it very near Group 1. The placing of the four clear-water lakes in Group 3 resulted primarily from the relative high abundances of *C. sphaericus* in these lakes (all greater than 73%) and the absence of *A. nana*.

Two lakes—Løgss (47) and Fraestes (55)—were classified as ponds and bogs on the bases of physical-chemical measurements but were placed in Group 1 by species groupings. In these cases the grouping was affected primarily by low
discriminant II scores (—4 in Løgsp and —9 in Praestø), which resulted from low abundance of species with high positive scaled vector values and relatively high percentages of those species with high negative scaled vector values.

Five polluted lakes were classified by this species group analysis in the clear-water group. All these lakes had P values bordering between Group 1 and 3—Bavelse Sø (4): 0.52 vs 0.48; Flynndersø (17): 0.51 vs 0.49; Hinge Sø (34: 0.56 vs 0.44; Tissø (72): 0.51 vs 0.49; and Tystrup Sø (75): 0.52 vs 0.48. A combination of fairly low percentages of _C. sphaericus_ (36—58%) plus the occurrence of some of those species generally found at clear-water sites accounts for these lakes being placed in Group 1. These lakes form a tightly spaced subgroup of points between groups 1 and 3 when plotted, with discriminant 1 values ranging from —0.6 to 0.7, and discriminant II values ranging from 12 to 17. The biological meaning of this subgrouping is uncertain, although all these lakes may be considered only mildly polluted.

The general lack of agreement between the 7 misplaced lakes of the Lake Grouping and the 13 lakes of Species Grouping strongly suggest a lack of direct correlation between the measured lake characteristics that define the lake groups and the relative chydorid abundances. Only two lakes were consistently misplaced: Store Gribsø (29) and Kalgaard Sø (40) were subjectively placed in Group 1 (clear-water lakes), but both were placed in Group 2 by the discriminant programs. However, the surprising amount of predictability among the species groups and the defined lake groups encourages one to believe that the true relationships of chydorid species to distributional factors are not far removed from ecological conditions that occur in these lake types.

**Species Diversity**

Species diversity of the 77 Danish lakes (Table 1) were calculated using the function $H = -\Sigma p_i \log_2 p_i$ (Shannon, 1949). This measure takes into account numbers of individuals within the sample as well as numbers of species (Lloyd & Ghelardi, 1964).

Biologically, one may equate diversity of chydorids to the complexity of their associations. This complexity is divisible into three areas (or habitats) of a lake: the littoral vegetation, and especially the submersent rooted aquatic, the littoral benthonic (including the entire bottom of shallower lakes), and the limnetic area. Evidence from collecting chydorids suggest that the littoral vegetation is the most suitable habitat for most species in this family; of secondary importance is the sediment—water interface, in which are found some of the larger species (_Alona afinis_, _A. quadrangularis_, _Leydigia leydigi_, and _Disparalona rostrata_). Two species may be found in the limnetic area ( _Chydorus sphaericus_ and _Alona rectangula_); these species are not freewimming, but probably use the planktonic algae as a feeding substrate. Hence the species diversity of chydorids reflects the approximate suitability of these three habitats.

There is a strong correlation between species diversity and a lake's trophic status (Whiteside & Harmsworth, 1967; Whiteside, 1968), which reflects the nature of the chydorid habitat. In lakes with low phytoplankton production, species diversity is always high, while in enriched lakes the values of species diversity are consistently low. A highly significant difference exists between the means of species diversity of the three lake groups (clear-water lakes, $\bar{x} = 2.72$; ponds and bogs, $\bar{x} = 3.01$; polluted lakes, $\bar{x} = 1.50$; $F = 33.32**$, df = 2, 74). The major source of difference is between Group 2 and 3 (LSR$_{0.05} = 1.45 < 1.51$), and an observable difference exists between Groups 1 and 3.

Mathiesen (1966) had shown a relationship between trophic level and depth to which macrophytes grow, as well as an association of certain plant types with different levels of production. These findings help explain the negative correlation of chydorid diversity and trophic level. In the more polluted lakes (high phytoplanktonic production), a lesser variety of rooted aquatics is found, thus decreasing available habitat for the bulk of chydorid species. If we assume that chydorid distributions, as with other animals studied from this approach (MacArthur & MacArthur, 1961; Pianka, 1967), are governed primarily by the diversity of available habitat, then a dependence on macrophytic vegetational structure is expected. Therefore, in strongly polluted sites [e.g., Fredriksborg Slotsø (18), Pedersborg Sø (54), and Søllerød Sø (69)] one would expect to find the lowest Shannon-Weaver values ($H$).

In those lakes of extreme pollution (mean phytoplanktonic production greater than 500 g C/m²/yr: Table 1), the benthic species average only 7% of the total population, while the limnetic species average 87% (Table 13). In all these lakes, with the exception of Bavelse Sø, chydorids not restricted to littoral vegetation comprise more than 90% of the community. Hence it is evident that the chydorid diversity is dependent primarily on
the relative abundance of the two species that can occur in the plankton—*C. sphaericus* and *A. rectangularis*. The benthic species are not affected by pollution so much as are those that inhabit the littoral vegetation.

**Discussion**

Goulden (1966) in a brief summary of cladoceran remains in lake sediments, emphasizes the importance of examining modern-day assemblages in order to discover what the fossil records for individual species represent. The present study of chydorid remains from the surficial sediments of 77 Danish lakes attempts to find what relationships exist between chydorid communities and lake type, and to ascertain what factors are important in controlling the distribution and abundance of chydridors.

From the surficial sediments of these Danish lakes, which show a wide variety of physical-chemical measurements (Table 1), 35 chydorid species were recovered. Twenty-two species occurred in at least 19 of the 77 lakes (Table 8), while 13 species were considered infrequent (Table 9). Evidences from the data provided in Tables 7–9 indicate that *Chyodus sphaericus*, *Alona rectangular*, *Leydigia aphanoceroides*, and *Acroroperus angustatus* are most common at polluted sites. The first two species probably exist in the plankton and may be considered indicators of pollution, especially when occurring in large relative abundances. The two latter species are fairly rare in Danish waters, and their preferred habitat is unknown, although it is most likely the muds of the littoral.

Other, more common species regarded as benthic are *Alona quadrangularis*, *A. affinis*, *Leydigia leydi*, and *Disparalona rostrata*. These species exist primarily in the bottom muds, so they are not so severely affected by pollution (Table 13). Hence, although they are not regarded as pollution indicators, they do occur at enriched localities. The majority of chydorid species prefers conditions found in clear-water lakes or in ponds and bogs, where *Alonella nana*, *A. excisa*, *A. exigua*, and *Graptoleberis testudinaria* typify the assemblages. The clear-water lakes possessed most of the species found at ponds and bogs (but in lower relative abundance), and pollutional species occasionally occurred in high percentages in these lakes. It is suggested that the major factor controlling the distribution of chydorid species is the habitat available to a particular species; this conclusion is based on a marked decrease in number of chydorid species at polluted sites, where submergent rooted aquatic vegetation (used as substrate by most chydoridors) is lacking.

Discriminant analysis was selected as a tool for defining lake types, which lead to 3 objectively definable lake groups—clear-water lakes (Group 1), ponds and bogs (Group 2), and culturally affected (polluted) lakes (Group 3). Processing the data by discriminant program provided an objective classification of lakes based on the 7 lake characteristics used. This in turn provided a framework for exploring the chydorid associations within each group.

With the 22 most common species as variables in the discriminant analysis, the differences between the 3 lake groups were statistically significant. The differences between species composition of these lake groups were then used to define 3 lake groups based on relative percentages of chydorid remains. A fairly high degree of compatibility (0.83) occurred between the lake types formed by these two approaches, i.e., 83% of the time the lake type predicted by discriminant species analysis corresponded to the lake type defined by discriminant lake analysis.
Fig. 2. Relative percentages of the 22 most common chydorid species in Denmark from 25 selected lakes which typify each discriminant group. Group 1 lakes have a sub-group, represented by Esrom and Fure lakes, in which littoral species are not so important as the main group. Group 2 lakes include ponds and bogs which are difficult to distinguish between on the basis of chydorids. Group 3 also has a sub-group by having high percentages of the planktonic chydorid, \textit{Alona rectangula}. The P-values are the probability of each lake belonging to its respective group.

Fig. 2 illustrates “typical” assemblages from each lake group and graphically points out the differences detected by multiple discriminant analysis. Group 1 chydorid assemblages differ from Group 2 by having higher percentages of \textit{Chydorus piger}, \textit{Camptocercus rectirostris}, \textit{Alonopsis elongata}, and \textit{Monosiphon dispar} and lower percentages of \textit{Graptoleberis testudinaria}. Groups 1 and 2 differ from Group 3 by having a more equitable distribution of species; also, Group 3 has higher percentages of \textit{Chydorus sphaericus}, \textit{Alona rectangula}, \textit{Leydigia leydigi}, and \textit{Pleuroxus trigonellus}.

Within Group 1, species are fairly evenly distributed. The subgroup represented by Esrom and Fure lakes have larger percentages of the benthic species \textit{Alona affinis} and \textit{A. quadrangularis}. These lakes illustrate the effects of lake morphometry upon the chydorid assemblages found in the lake. Both lakes have large, “U-shaped” basins, with a relatively small littoral area. In such lakes the littoral communities are not so well developed, and benthic elements become more important. In Group 2 lakes the similarities in chydorid populations between bogs and ponds can be seen. Group 3 also contains a sub-group, Arresø, Gurre Sø, and Lyngby Sø, which is characterized by high percentages of the planktonic \textit{Alona rectangula}. Most Group 3 lakes have high percentages of \textit{C. sphaericus}, with few other chydorid species represented. Hinge Sø and Silkeborg Langsø were included in Figure 2 to show the effects of higher percentages of \textit{Alona quadrangularis} on the p values. Fig. 2 is valuable in helping to understand the distinctions made between groups by the discriminant analysis.

It is possible that multiple discriminant analysis may be useful to paleolimnology, because the methods employed for obtaining the relative abundances of the chydorids in this study are identical to those used in core studies. An investigator could substitute in the discriminant function the relative percentages of the pertinent chydorid species found in cores of lake sediments and obtain a reasonable probability value as to the lake type from which the chydorid population derived. Comparisons between chydorid associations at different periods of a lakes development will enable an objective, reasonably accurate description of conditions present at different periods of the lake’s history.
Future core studies on chydorids will become more meaningful when those factors that are important in the distribution and abundance of these animals become known, for then these factors can be used to form new discriminant equations to define the lake groups more precisely. This will improve the predictability of lake type based on species abundance and consequently lead to more meaningful interpretations of biostratigraphic studies of lake sediments.

The application of discriminant analysis to paleolimnology is potentially extremely useful, in that it is not limited to those parameters used in this study. A series of lakes from any region can be analyzed on the basis of those biological, chemical, and physical characters that are measureable and of interest to the investigator. Once discriminant groups have been defined (and tested for their definitive value), remains of any group of animals (not only chydorids) or plants (such as diatoms) can be used.

The significance of chydorid species diversity is not yet fully understood. Goulden (1966) first used the Shannon-Weaver index of diversity to ascertain how closely the chydorids approximated the MacArthur type-I distribution of species numbers in a population (MacArthur, 1957). Finding a progressively better fit to the model toward the top of the core of sediments, he concluded:

"... after formation of the aqua, the chydorid population progressed towards maturity (seen at 20 and 16 cm) as measured by the proximity to the expected type 1 species distribution. A sudden increase in productivity, resulted in a poor approximation to the type-I species distribution and therefore decreased maturity. However, the population quickly recovered from this alteration of the environment and gradually developed towards an almost completely mature condition as seen in the fossil population of the surface sediments (1.5 cm level)."

There are several criticisms of the application of this model to chydorid remains in sediments because the biological assumptions inherent in this model may not be applicable to chydorid assemblages. Although no population studies of chydorids have been conducted in nature, it is difficult to imagine that chydorids occupy contiguous, nonoverlapping niches maintained through competition. Goulden's assumption (p. 393) that this competition is for food resources seems unlikely (Fryer, 1968). Furthermore, Cohen (1968) has shown that the same distributional patterns are obtained from at least two other mathematical models involving different biological assumptions. Hence there seems to be little reason to interpret the fit of chydorid populations to these distributions until more detailed information is obtained on their ecology.

A further application of species diversity indices in paleolimnology was attempted by Whiteside (1968), where the highly significant inverse correlation found between primary production and chydorid species diversity was suggested as a tool to indicate past productivities at different times in a lake's history. The inverse correlation is evident, and therefore its use is justified, but the underlying causes of such a relationship are still unknown. Future studies should explore this relationship, as there is probably a more complex system operating than suggested earlier.

Goulden (1964, 1966) found that chydorid diversity increased as the abundance of Cladocera in the sediments increased, and he attributed this phenomenon to increased lake productivity. The relationship between species diversity and production has already been discussed (Whiteside & Harmsworth, 1967), and Harmsworth & Whiteside (1968) have presented evidence suggesting there is no relationship between cladoceran abundance and phytoplanktonic productivity. Hence there seems to be no correlation between phytoplankton productivity and numbers of chydorid remains in sediments, but there is an inverse relationship between phytoplankton productivity and species diversity. A paradox still exists, however, in that in more cores studied the diversity and abundance of chydorids are usually positively correlated, whereas they are not in modern assemblages (Harmsworth & Whiteside, 1968).

The value of chydorids to paleolimnology are: 1) as they are a product of the lake in which they are found and not of external origin, all remains give direct indications of lake conditions, 2) they are abundant in most lake sediments, 3) they can be recovered from the sediments with relative ease, and 4) they are recognizable to species. It is apparent from the distribution of chydorid species over the range of lake types represented from the study area that chydorids have a wide range of tolerance to various chemical conditions. Patterns do emerge, however, when one considers not just their presence or absence but also their relative abundances. Unfortunately, a detailed knowledge of the factors that govern their distribution and abundance is still lacking. When this information eventually becomes available, subsequent studies on lake sediments will yield more definitive results.
In conclusion, too many biostratigraphic interpretations are misleading or of little value because of two interrelated things; 1) in very few instances are regional surveys undertaken to establish the present-day relationships of chyadorids to lake typology. This leads to 2) the overemphasis of world-wide species distributions applied to explaining local population phenomenon. This approach is limited because of genetic variations that may exist between species of different areas of the world (Shan and Frey, 1968), and the combined ecological factors affecting chyadorid species distribution cannot be identical for each area in which they are found.

SECTION II: CORE STUDIES

METHODS

Cores from Grane Langsø (27) and Esrom Sø (13) were taken by use of a modified Livingstone core sampler through 4-inch steel casing. A core 431 cm long was recovered from Grane Langsø through 11 m of water from a boat anchored at three points and secured by a line to two opposite shores. Coring was started through casing 10 m long. After approximately 3 m of core were obtained, the casing was forced 3 m into the sediment, and the remainder of the core was taken. Further lowering of the casing was prevented by a sand layer. The mud was extracted from the corer in the field, so that core recovery could be followed. Below the 431 cm of organic and sandy sediments was sand, which extended to at least 525 cm. Further penetration of the sediments was impossible. A supplemental core of the upper 60 cm in Grane Langsø was taken adjacent to the main coring site. This section was quite watery, and subsamples were taken at 5-cm intervals immediately following extraction from the corer.

Esrom Sø (13) was cored near station II of Jónasson (1961). Water depth was 21 m. Coring was done from a platform constructed over two boats; 6 anchors were used to stabilize the platform. A procedure identical to that at Grane Langsø was followed.

The core sections were stored in a refrigerator at the Freshwater Biology Laboratory in Hillerød until subsampled. Each subsample was divided into two portions, one for chyadorid analysis and the second for pollen counting. The subsamples for chyadorid analysis were processed in the same way as the surficial samples, as outlined in Section 1, except for the sand layers in the Grane Langsø core, where a larger quantity of material had to be treated because of the scarcity of chyadorid remains.

The second portion of selected subsamples was treated for pollen analysis following the acetolysis-HF procedure of Faegri & Iversen (1964). Processed samples were stored in glycerol. Counting of pollen from Grane Langsø was conducted under the supervision of Svend Andersen of the Danish Geological Survey, and his help is greatly appreciated. Counts of 200 AP grains were made to establish pollen zones at various levels of the core. Counts of pollen from Esrom Sø were done by Vernon Rampton at the Limnological Research Center of the University of Minnesota.

Four carbon-14 dates were made on Grane Langsø by the radiocarbon laboratory at Indiana University. A fifth date was made by Dr. J. G. Ogden at Ohio Wesleyan University. No radiocarbon dates were made on the Esrom Core, as the carbonate content of this core was extremely high.

GRANE LANGSØ

INTRODUCTION

Grane Langsø (27) occupies a kettle in the stratified drift of a subglacial stream of Baltic glacial age. Nygaard (1965, p. 14) considers this lake a “typical seepage lake,” with no apparent surface streams feeding or draining the lake. Thus the sediments of this basin are primarily a direct consequence of events confined to the small drainage area of the lake.

The core was taken from the northern half of the lake, approximately equidistant between Hansen's 1965 borings IX and X.

STRATIGRAPHY

Fig. 3 includes a diagrammatic representation of Grane Langsø sediments. A brief description of each sediment type follows:

Sand (431–525 cm). A coarse, angular sand which contained charcoal bits and clay lumps. This sand probably extends well below maximum penetration of the Livingstone corer and represents subglacial deposits.

Gyttja (357–431 cm). A compact organic layer with low water content. This gyttja appeared to have a higher clay content than the uppermost gyttja.

Sand (279–357 cm). This upper layer of sand was a medium to very-fine-grained sand (Hansen, 1965) containing organic lenses (sandy gyttja) at various depths. This sand is at the level of
maximum penetration by Kaj Hansen (1965), who attributed the sand to eolian action.

**Sandy gyttja (267–279).** Hansen (1965) reported the organic carbon content of this layer was less than 25% and referred to this layer as "grey sandy silt" or "grey silt." The sandy gyttja merges at the top with silty gyttja; the exact point of contact of these layers is indistinct.

**Silty gyttja (264–267 cm).** Hansen (1965) referred to this layer as "dark silty gyttja," it was 10 cm thick in his boring X (Fig. 3). It represents a transition between sandy gyttja and gyttja.

**Gyttja (0–264 cm).** This material comprised the major portion of the core. It was olive grey-green, composed primarily of organic detritus, with plant fragments frequent. Water content decreased with depth.

Chydid Assemblages

A total of 29 species was recovered from Grane Langsø sediments. With the exception of *Alona costata*, all 22 of the "most common" species of Section I were found. In addition, 8 species considered infrequent in Denmark were recovered. *Alona intermedia* was the most abundant of the infrequent species, with a maximum percentage of 7.5% at 400 cm; others, which seldom exceeded 2% of the total chydid assemblage, include *Acroperus angustatus*, *Pleuroxus laevis*, *P. aduncus*, *Camptocercus illijeborgii*, *Pseudochydrus globosus*, and *Percantha truncata*. Fig. 4 lists the 21 common Danish species (note omission of *Alona costata*) found in Grane Langsø sediments, following the format of Fig. 2 (Section 1). Included in Fig. 4 are diagrammatic changes of chydid habitat type (after Table 13) and of species diversity in the core.

Three species, *Alona rustica*, *Chydrorus sphaericus*, and *C. piger*, were present at most levels in Grane Langsø sediments. The tuberculate forms of these species, although not confined to sandy layers, predominated in these levels. The unusual forms of *C. sphaericus* are not truly tuberculate but display a plate-like arrangement on the valve surface (Fig. 5).

Two assumptions are inherent when chydidors are used to interpret past lake conditions. The first is that chydidors are ecologically stable, i.e., those factors important in the distribution and abundance of the fossil assemblages are essentially identical to factors that control them today. Chydidors studied by Frey (1962) from last interglacial (Eemian) deposits in Denmark were morphologically identical to those species recovered today. Furthermore, he found that the relative abundance of species recovered from the Eemian, which presumably had a climatic regime similar to today's, was similar to that of present-day forms. The data from Tables 8 and 9 (Section 1) produce a highly significant correlation with the Eemian data (Spearman's rank correlation coefficient, $r_a = +.86^{**}$, Fig. 6).

The second assumption is that chydidors respond to changes induced by climate or man. DeCosta (1968) found close agreement between pollen zones and chydidonal faunal zones in a core of lake sediments from Wyoming, and Goulden (1964) correlated changes in Cladoceran stratigraphy with both climatic and cultural events.

Discriminant Analysis

The discriminant function generated with the use of chydidor species as variables (Section 1) was applied to characterize the species assemblages in Grane Langsø sediments. The 22 "most common" species were used as variables in Grane Langsø. A discriminant score was calculated for each level of the core, and probability values were assigned. The results were somewhat surprising, in that $P$-values derived from different levels of the core varied without any apparent biological mean-
FIG. 4. Relative percentages of the 21 most common species found in Grane Langsø, Denmark, sediments following the format of Fig. 2. This figure also includes pollen zones, radiocarbon dates, stratigraphy, faunal zones, species diversity values and habitat type of each level. Pollen zones, radiocarbon dates, stratigraphy, and the formation of faunal zones are discussed in the text. Species diversity values (Shannon-Weaver indices) are plotted to show changes throughout the core. Habitat type is the total percent of benthic, littoral, or limnetic species (see Table 13).

ing, i.e., adjacent levels (presumably from similar faunal zones) were not grouped together. These results have led to a re-evaluation of multiple discriminant analysis as a tool in paleolimnology.

Failure of the multiple discriminant analysis to sensibly classify levels from the Grane Langsø sediments was directly related to the sensitivity of chydorids to climatic change. In treatment of the surficial data (Section I), it was logical to assume that the statistical populations were identical. The variations were related primarily to 1) the chemical element of the environment, and 2) physical elements, including habitat, lake morphometry, and benthic substrate. Climate was eliminated as an important variable, for the climate of Denmark is essentially uniform throughout.

Grane Langsø is a small lake, relatively poor in chemical nutrients (Table 1), thus very sensitive to external disturbances. Climatic change could have had either a direct effect (such as change in moisture or temperature) or it may be viewed as a varying framework within which biotic interactions or human activities influenced the character of the lake. Thus a component not considered in the lake survey was added, and the statistical changes of the chydorid populations must be reconsidered on a different basis. Core assemblages contain species that are evidently unimportant in modern-day lakes (Table 10—scaled vectors), but which make up a considerable percentage of the population in the sediments.

**POSTGLACIAL HISTORY**

The core section represented in Fig. 4 may be divided into 5 faunal zones, based on the relative abundances of chydorid species.
Faunal zone 1. Grane Langsgå basin resulted from melting of a large ice block in a tunnel valley. The earliest deposits (below 431 cm) were sand from late-glacial streams. *Alona affinis* and *Chydorus sphaericus* were the two most important species found in this sand, along with *Alona quadrangularis*, *Acroperus harpae*, and *Alonella nana*. Most likely these assemblages were remnants of populations from small, temporary ponds within the basis. These ponds were not suitable for development of littoral vegetation and stable lake conditions.

The chydrorid counts from the gyttja at 430 cm and upward to 410 cm represent the true pioneer species at Grane Langsgå—*Alonella nana* (30%), *Chydorus sphaericus* (25%), *Alona affinis* (10%), *A. quadrangularis* (9%), and *A. rectangula* and *Acroperus harpae* (6%). The bottom dwellers and limnetic species (Table 13, Section I) make up 77% of the chydrids at 420 cm and 68% at
410 cm, and the lake habitat probably lacked rooted aquatics. This lack could have been the result of lower transparencies due to high organic content in the lake water. An analogy to a present-day site is difficult, but certainly these early chydorid communities are similar to those found in some Danish ponds today. For example, Råbaerg Sø (57, Table 1, Fig. 2), a pond located northwest of Aalbaek at the northern tip of Jutland, has a very similar chydorid fauna. This pond lies in a sand dune region and has no surface outlet.

The chydorids of faunal zone 1 thus represent a pioneer stage. The landscape around Grane Langsø at this time (+9500 BP I.U. No. 56) became stabilized with the pioneer tree species (Betula and Pinus) of pollen zone IV (Fig. 7).

**Faunal zone 2.** Faunal zone 2 is marked by increased percentages of littoral chydorid species *Rhynchotalona falcata, Pleuroxus trigonellus, Graptoleberis testudinaria,* and *Chydorus piger* (Fig. 4). The implied increase in variety of chydorid habitat is coincident with the shift from pollen zone V to VI (Fig. 7), which represents normal succession of tree species resulting from

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**Grane Langsø, Denmark**

**Pollen sequence, zones and radiocarbon dates of lake sediments**

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**Fig. 7.** Relative percentages of tree pollen recovered from the sediments of Grane Langsø, Denmark, and radiocarbon dates from four levels of the core. Pollen zones were assigned on the basis of the pollen counts and the dates.
continued climate amelioration (Iversen, 1960). The upper part of faunal zone 2 represents the late Boreal period, with a radiocarbon date of 8044 ± 582 yrs. BP (I.U. No. 57). This faunal zone extends to the top of the gyttja contact (357 cm). At 382 cm a slight change in sediment type was accompanied by an increase in percentage of *Pleuroxus trigonellus* (Fig. 4), implying a very short enrichment phase (see discussion in connection with faunal zone 4b).

**Faunal zone 3.** Faunal zone 3 is characterized by high percentages of *Chydorus piper* and a maximum of *Alona rustica*. It includes the more inorganic levels (357–264 cm) of the core. Pollen counts from 330 to 270 cm were placed in pollen zone VII (Fig. 7), and the levels 357–267 cm represent Atlantic time.

The lenses of sandy gyttja within pollen zone VII had chydorid assemblages differing from the sandy layers, and the lake was probably more eutrophic during these intervals, as evidenced by increased percentages of *Pleuroxus trigonellus*.

No modern Danish lakes have *C. piper* with abundances comparable to those found in Grane Langsø during the Atlantic period. Frey (1962) postulated that increased *C. piper* percentages corresponded to the development of acid conditions within a lake, and Harmsworth (1968) recovered tuberculate shells almost exclusively from peaty sections of a core (Blelham Tarn, England). In Grane Langsø the high percentages of *C. piper*, plus the increased frequency of tuberculate chydorids in sandy layers (Fig. 5), suggest that bog or acidic conditions were prevalent.

The sandy gyttja marks the transition between pollen zones VII and VIII, and the silty gyttja is most likely Sub-Boreal in age (264–267 cm). A section of core 260–267 cm was dated as 4560 ± 219 BP (I.U. No. 59), suggesting late Atlantic or early Sub-Boreal time. Iversen (1960) believes the boundary between pollen zone VII and VIII resulted from climatic change. Climate was the primary factor affecting changes in sediment type at this boundary, for one would expect man to have caused a more abrupt change in sediment type.

**Faunal zone 4.** The core section 264–50 cm is subdivided into 4a (254–190 cm), 4b (190–145 cm), and 4c (145–50 cm). The chydorids of 4a and 4c are quite similar, with *Alona affinis, A. quadrangularis, Chydorus sphaericus, Acroperus harpae, Rhynchotalona falcata,* and *Graptoleberis testudinaria* maintaining fairly constant percentages. The intervening zone (4b) has high percentages of *Pleuroxus trigonellus*. Pollen counts (Fig. 7) place the levels between 250 and 50 cm within pollen zone VIII (Sub-Boreal time). Anomalous radiocarbon dates of 5930 ± 464 BP (I.U. No. 58) and 3830 ± 205 BP (O.W.U. 336) were made at 157–177 cm.

In 4a, chydorid percentages are evenly distributed, and during much of this time Group 1 type chydorids predominated. Chydorid communities in Grane Langsø were probably similar to those of today except for the higher percentages of *R. falcata*.

Above 190 cm a change in the major chydorid species begins, accompanied by a slight alteration in sediment lithology. From 190 to 145 cm (zone 4b) the predominant chydorid species is *Pleuroxus trigonellus*, which before and after was a relatively unimportant component of the chydorid assemblage. The increase of *Pleuroxus* cannot be explained by information from Table 8 (Section I); however, lowest species diversity averages in 4b, and Whiteside (1968) presented evidence pointing out an inverse relationship between chydorid species diversity and phytoplanktonic primary production.

The 170–cm level within 4b has lower *P. trigonellus* abundance, accompanied by an increase in *Alona rectangula* percentage. The core section from which this level was subsampled extended from 93 to 177 cm, so contamination is doubtful. The sediment is more compact or clayey. It is probable that the variations at 170 cm represent real changes in the lake’s condition.

The increase of *Alona rectangula* at 170 cm could be the result of man’s activities in the watershed. High percentages of *A. rectangula* resulted in a shift towards limnetic faunas (Section I); they suggest less extensive littoral habitat and (as species diversity dropped) greater phytoplanktonic production. This level (170 cm), and also an analogous level at 80 cm, are interpreted as representing short enriched stages in Grane Langsø history.

Both the pollen evidence (Fig. 7) and the other data indicate that the radiocarbon dates for the sediments between 157 and 177 cm are too old. This may be due to analytical error or to redeposition of carbon from older sediments. A decrease in precipitation during the Sub-Boreal could result in re-deposition in the benthos of older lake deposits exposed along the lake’s margin. This explanation is supported by large pieces of vegetation incorporated in the sediment at 157–177 cm. A lower water level might thus explain the anomalous dates and also have an en-
richment effect upon Grane Langsø. Man’s activities in the lake’s environs would add to the enrichment during this period. Kaj Hansen (1965, Fig. 7) has also concluded that Grane Langsø was more productive during the Sub-Boreal. Hence, the increase in Pleuroxus trigonellus is attributed to increased productivity in the lake. The occurrence of P. trigonellus from other sections of the core, mentioned earlier, are also interpreted as indications of enriched conditions.

Above 145 cm is zone 4c, which is similar to 4a. The increase of Alona rectangula at 80 cm is interpreted as a phase of increased production. The date of 1600 years ago for this eutrophication phase is estimated from a sedimentation rate of 0.53 mm/yr. Zone 4c extends up to 50 cm, a level correlated with pollen zone IX.

**Faunal zone 5.** Faunal zone 5 extends from 50 cm to the top of the sediment. This zone is characterized by increased percentages of Alonella nana and Alonopsis elongata and decreased percentages of P. trigonellus. The pollen count at 50 cm was assigned to pollen zone IX (Sub-Atlantic time), which encompasses faunal zone 5.

Alonella nana is associated with low alkalinites (Whiteside, 1968), and the abundance of Alonella (>30%) probably reflects a chemical change at Grane Langsø. The surficial sediments, however, do not have A. nana so abundant (Fig. 2), suggesting a change within the past 100 years (again assuming a sedimentation rate of 0.53 mm/yr.).

Chydorid species diversity is fairly constant throughout the core (Fig. 4); values range from 3.95 at 70 cm to 2.13 at 420 cm, with an average of 3.34. Low values were found for the sand levels. The predominant species of 4 levels in the upper sand were Chydorus piper (range 26–54%), C. sphaericus, Alona affinis, and A. quadrangularis, and at some levels A. rustica and Acroperus harpae (Fig. 4). The lower species diversity values are due primarily to the increased relative abundance of C. piper. In the lower sand, A. affinis dominated the species spectra, with A. quadrangularis and C. sphaericus of secondary importance. Low diversity values at 80 cm reflect an increased abundance of Alona rectangula (22.5%) and Chydorus sphaericus (14.5%). Low values at 410 and 420 cm are due primarily to the abundance of Alona affinis. The lowest count from the organic sediment at 430 cm reflects the dominance of Alonella nana, with C. sphaericus next in importance—these two species account for 55% of the chydorid assemblage. Alona affinis, A. quadrangularis, and A. rectangula make up another 29%.

Species diversity values of chydorids reflect the nature of their habitat at different periods in the lake’s history. The fluctuations of the diversity values can be related to 1) lithologic changes in the sediments, i.e., lower values in sandy layers, and 2) changes in the lake which were not noticeable in the gross stratigraphy but which are recorded as faunal shifts. The latter changes in species diversity may be termed biotic shifts. They occur at 80 cm, in faunal zone 4c, and at 410–430 cm. Low diversities at 80 cm were interpreted as a result of increased lake production. The changes at 410–420 cm suggest an environment lacking rooted aquatics.

**Esrom Sø**

**Introduction**

Esrom Sø (13), Denmark’s second largest lake, with an area of 1730 ha, is situated northwest of Hillerød, on the island of Zealand. The lake extends north-south, occupying a basin in the morainal topography adjacent to Gribskov forest. Esrom Sø has few bays or peninsulas and has rather steep shores, so rooted aquatic vegetation is scarce. The lake basin is characterized by a regular slope and by an extensive and flat lake floor, without submerged banks or depressions (Jónasson & Mathiesen, 1959). There are no large streams serving Esrom, and Berg (1938) calculated a residence time of 7.5 years for Esrom water.

**Stratigraphy**

It was not possible to sample effectively the upper 50 cm with a Livingstone corer; these sediments were sampled with a stratified bottom sampler designed for Esrom Sø (Berg, 1938, p. 157). Maximum penetration of the sediments was to 881 cm, where glacial till was encountered (Fig. 8).

Above the till (840–380 cm) was calcareous clay, followed by calcareous gyttja (380 cm to the top). Lithologic analyses conducted by Kaj Hansen (1968) are outlined below.

**Glacial till** (881–840 cm). The glacial till was dark gray and very sandy when fresh but light gray and hard when dried. Only sharp calcite and other mineral grains were observed under the microscope. A relatively large pebble was noted at 870 cm, along with several smaller pebbles. The calcite content of the till was 22% (Fig. 8). Following a treatment with HCl, a particle-size analysis was made on the lower 4 m. The lowest glacial till had the greatest sand content (grains 62 μ = 60%), but decreased to 2% at the upper limit of the till (Fig. 8).
Esrom Sø, Denmark

![Core Stratigraphy](image)

**Fig. 8.** Core stratigraphy of 881 cm of Esrom lake sediments (after Hansen, 1968). The diatom curve is calculated from the relative amounts of alkali-soluble SiO₂ present.

_Calcareous clay_ (840–340 cm). The clay was grey and soft when fresh but light grey and very hard when dried. The border with the underlying till was sharp. There were numerous layers of fine sand, and at 554 cm a 3-cm-thick layer of coarse sand. The carbonate content of the clay ranged between 20 and 30% (Fig. 8). Preparations observed under the microscope showed small grains of quartz and calcite of silt size (8–16 μ), but at 650 cm coarse silt (16–31 μ) dominated, and at 500 cm fine sand.

_Calcareous gyttja_ (340–0 cm). The fresh gyttja was olive-green, soft, and gritty; when dried, it turned white and hard. The gyttja consisted primarily of small calcite grains and diatoms, with smaller amounts of other mineral grains and fine, structureless organic detritus. The carbonate content increased to 74% at 395 cm and 79% at 305 cm, followed by a decrease to 59% at 250 cm.

**CHYDORID ASSEMBLAGES**

A total of 30 species of chydorids was identified. All of the “most common” species of Section I were found, and representatives of these species formed the bulk of the chydorid abundances (Fig. 9). The other 8 species found never exceeded 2% of the total percentages of chydorids at any level. Six species (*Pseudochydorus globosus*, *Camptocercus lilljeborgi*, *Acroperus angustatus*, *Percantha truncata*, *Kurzia latissima*, and *Anchistropus emarginatus*) were identified from only a few levels in the sediments, while *Pleuroxus laevis* and *Leydigi acomthoceroides* were both found at more than 8 levels.

The predominant chydorid species in Esrom sediments were *Alona affinis* and *A. quadrangularis*, which combine to make up approximately 50% of the chydorid spectra throughout most of the core (Fig. 9). Other species, not so abundant, were *Acroperus harpae*, *Eury cercus lamellatus*, *Graptoleberis testudinaria*, *Camptocercus rectirostris*, *Pleuroxus uncinatus*, and *Monospilus dispar*. Infrequent species were *Alona guttata*, *A. rustica*, *Alonella exigua*, and *Pleuroxus trigonellus*.

**DISCRIMINANT ANALYSIS**

Esrom lake, with its deep, U-shaped basin, large surface area, smaller littoral area, and richer waters, provided a situation where the effects of climate on the chydorid stratigraphy were not so important as in Grane Langsø. For this reason the results of discriminant analysis were useful. At all but four values, P-values placed the chydorid assemblages in Group 1 (clear-water lakes). One level (60 cm) was scored as a Group 3 lake, while 3 others (310, 360, and 370 cm) were scored as Group 2 lakes. The shift of littoral to benthic chydorid species at about 170 cm (Fig. 9) represents a shift towards the subgroup of Group 1 (Fig. 2). This shift was marked by the steadily increasing percentages of *Alona affinis* and *A. quadrangularis* and by the decrease of *Alonella exigua*, *G. testudinaria*, *Alonopsis elongata* and *R. falcata*; the last two species are important littoral components of clear-water lakes (Fig. 2).

**POSTGLACIAL HISTORY**

No faunal zones have been assigned to this core; instead the changes in chydorid percentages are interpreted as variations around a relatively constant chydorid assemblage type (Group 1).

The origin of Esrom basin may be analogous to the formation of dead-ice basins described by Florin & Wright (1969). Following the retreat of an active ice front, isolation of a large ice block remained in Esrom. Burial of this ice block by outwash provided insulation, thus decreasing wastage. During late-glacial time, small surface pools provided habitat for limited development of aquatic communities. The remains of these organisms are sparsely distributed in the calcareous clay (Table 14). The two levels in which abundant chydorids were found (450 and 550 cm). (Fig. 9) may represent phases of maximum development of these communities. Final melting of the dead-ice occurred during Pre-Boreal time. At 370 cm, which corresponds to pollen zone...
IV (Fig. 10), were *Acroperus harpae* (50%), *Chydorus sphaericus* (26%), *Alonella nana* (8%), and the two large *Alona* species, *affinis* and *quadranularis* (4% and 8%). These species were placed in Group 2 by discriminant analysis, so Esrom Lake must have been a shallow pond with some rooted aquatics.

This phase in Esrom's history was relatively short. Chydorid assemblages at 350 cm represent a transitional phase from Group 2 to Group 1 chydorids. At this level benthic *Alona* species increase in abundance, while *Acroperus harpae* and *Alonella nana* begin decreasing. Questionable data are obtained from pollen counts below 340 cm, because the high pine counts suggest poor preservation of other pollen types (Svend Andersen, per. comm.). I have assigned these levels to Boreal time, although no counts could be justifiably placed in pollen zone VI.

In late Boreal time, Esrom Lake acquired its present-day physical-chemical character. The apparent changes in CaCO₃ at 350 cm (Fig. 8) can be attributed to the diatom rise. Foged (1968), on the basis of the ecology of the diatom species recovered from this core, postulated a lake of relative high alkalinity throughout most of postglacial time.

The pollen counts of 340–310 cm were placed in zone VII (Atlantic time), and the chydorid community characteristic throughout most of Esrom's postglacial history was established. Chydorid assemblages were very similar to present-day abundances during Atlantic time (350–300 cm), and the littoral development of Esrom during this period was probably comparable, i.e., the littoral area was limited, as evidenced by the large number of benthic species (Fig. 9).

At approximately 300 cm an increase in diatoms (Fig. 8 and Foged, 1968) corresponded to the transition from Atlantic to Sub-Boreal time (pollen zones VII–VIII, Fig. 10). The apparent drop of CaCO₃ during this transition is not real, according to Kaj Hansen (1968); it merely reflected the increased importance of the
diatoms—no real changes in CaCO₃ content of the sediments occurred until the upper meter of sediments (Fig. 8, and Berg, 1938).

Littoral species were more important from 300 cm (Fig. 9) to about 160 cm, implying increased rooted aquatics during Sub-Boreal time. This increase could have come through increased transparency or a slightly warmer climate or, most likely, both. The abundance of littoral species was still less than normally found in most clear-water Danish lakes, exemplifying the importance of morphometric factors in determining the abundance of chydorid species, for even at maximum development the U-shaped basin and the lack of bays limited the available habitat.

Above 160 cm benthic species again predominate. Several littoral species are either absent or rare above this level (Alonella excisa, Graptoleberis testudinaria, Alonopsis elongata, and Rhynchotalona falcata). The pollen count at 150 cm was placed in zone IX, or Sub-Atlantic time. The shift in chydorid habitat type could be the result of the cooler, wetter climate of the Sub-Atlantic period, causing poorer growth of rooted aquatic vegetation—thus creating a sparse littoral habitat. Lower values of species diversity reflect the loss of littoral chydorid species.

At 60 cm Esrom became more enriched, and production increased. Carbonate content of the sediment decreased as a result of decreased oxygen in the lake's hypolimnion (Whiteside, 1965) (Fig. 8), in turn the result of the inferred increase in production. Species diversity values decrease slightly, and benthic chydorid species become increasingly important (Fig. 9). The clearing activities in the Early Middle Ages in Esrom's environs suggested by Wolthers (1956) could account for this change in trophic status.

Fig. 9 reflects the remarkable fidelity of Esrom chydorid populations to the clear-water lake group. This observation confirms the opinion that distinct faunal zones need not be applied in all situations to describe or clarify changes in the lakes' history. After the early development, Esrom Lake has always had the ecological components characteristic of Group 1 lakes.

Diversity indices of chydorid remains ranged from 1.89 at 370 cm to 3.67 at 190 cm, with a mean of 3.36. The low value at 370 cm reflects the high abundance of Acroperus harpae (Fig. 9). Above 370 cm, to approximately 150 cm, diversity values are greater than 3.00. At 150 cm values fall below 3.00 and remain below this figure throughout the remainder of the core. The latter decrease corresponds to the absence of littoral species in the upper sediments.

**Concluding Remarks**

The present-day characters of Esrom and Grane Langsø lakes are strikingly different. Esrom Sø is in a large, U-shaped basin and has alkaline waters, while Grane Langsø is small and nutrient-poor. The chydorid development of Grane Langsø was found to be very sensitive to climatic or cultural change, because of the delicate chemical balance of the lake. In Esrom, fossil chydorid assemblages varied little, because of the dampening effect of morphology of the basin and the relative chemical stability of Esrom's lake water. The minor shifts observed were related primarily to climate but also to man's activity during the Middle Ages.

The most important factor causing changes in both lakes was climate. In Grane Langsø the lake responded quickly, and multiple discriminant analysis was of little use. In Esrom, where the effect of climate was negligible, the discriminant analysis was an effective tool. Multiple discriminant analysis is useful if all factors determining distribution and abundance of chydorids are realized and incorporated into the function.
Esrom Sø Denmark

Pollen sequence and zones of lake sediments

Fig. 10. Relative percentages of pollen recovered from the upper 4 m of sediment from Esrom Sø, Denmark. Pollen zones were assigned on the basis of the pollen counts. No counts were made on glacial sediments, because of poor preservation and scarcity of material.

under such conditions objective conclusions can be made concerning past lake conditions.

Multiple discriminant analysis is analogous to the niche hypervolume (Hutchinson, 1957), in which the parameters used to generate the discriminant function form the dimensions of the hypervolume. The more accurate an investigator pinpoints the important factors (abiotic and biotic) affecting distribution and abundance of organisms (and uses these factors to generate the discriminant function), the more accurate will be the description of that organism’s niche. Thus multiple discriminant analysis provides a framework for an orderly analysis of a species’ niche. Furthermore, the discriminating planes (discriminant axes I & II) will maximize differences among groups (species). Alterations of the parameters used to describe the function change the relative importance of each parameter (scaled vector) so that, by altering these parameters, one can gain more insight into the relative importance of each variable operating under varying ecological conditions.

Sedimentation rates, based on pollen zonation, can be estimated for both lakes. In Grane Langsø the gyttja, 430–357 cm, represents a time interval 9500–7500 yrs BP, with a sedimentation rate of 0.37 mm/yr. The sand gyttja contact (357 cm) may be analogous to contacts of sand-peat from neighboring peatbogs (Jesson, 1939). The 90 cm of sand covers the time interval 7500–5000 yrs BP (Atlantic time), or 0.36 mm/yr. The upper gyttja has the greatest sedimentation rate, 0.53 mm/yr.

In Esrom, the basal 90 cm (pollen zones IV–VII), accumulated at a rate of 0.12 mm/yr. During the Sub-Boreal it was 0.68 mm/yr, and most recently (pollen zone IX) it was 0.57 mm/yr.

The differences observed between Grane Langsø and Esrom Sø bring forth a valuable point to consider for paleolimnologists. What are the goals of the paleo-study? If one wishes to study
chydorid community development, then he should choose a lake in which maximum development of chydorids can be expected—such a lake was Grane Langsø. On the other hand, if the lake is the focus of the study, a decision has to be made as to whether the chydorid data add greatly to information, or will some other fossil type—such as diatoms or midges—reflect changes in lake history more effectively. Chydorids are valuable indicators of littoral development, and much information can be gained concerning the history of a lake's littoral zone. Changes in the littoral may imply lake changes, as at Grane Langsø, or may represent only minor variations, as at Esrom.

Data from the core studies add some information to the disputed boundary between pollen zones VII and VIII (Iversen, 1960). The main point of contention is whether the boundary (represented by declines in elm and lime pollen) was the result of climatic or cultural influences. The data from Esrom and Grane Langsø suggest that a climate amelioration occurred during the Sub-Boreal. This amelioration was reflected in Esrom Lake by increased diatom production (Fig. 8; Foged, 1968) and by greater littoral development (evidenced by chydorids, Fig. 9). At Grane Langsø the shift from sand to gyttja deposits marks the transition of pollen zones VII–VIII; this marker is not likely to be the result of cultural activities, as it occurs at several Jutlandic sites. In addition, chydorid assemblages are most diverse and most stable during the Sub-Boreal (with the exception of faunal zone 4b), thus suggesting ideal growing conditions within the lake. Hence, the evidence from these lakes supports a climatic change for the zone boundary.

Within the family Chydroridae, there are certain species that may be considered pioneer species in northern Europe. Gouldean (1964) found the first chydorid species in late-glacial sediments of Esthwaite Water (England) to be Chydrorus sphaericus, Acroperus harpae, Alona affinis, A. quadrangularis, Campiocerco rectirostris, and Alonella nana (listed in decreasing order of abundance). Harmsworth (1968) found Alona affinis and Alonella nana the most important component of late-glacial Blelham Tarn (England), and Alonella nana and Acroperus harpae the pioneers from postglacial sediments. In Grane Langsø, late-glacial sands had primarily Alona affinis and Chydrorus sphaericus present, while in the first organic sediments of the postglacial sediments chydorids species ranked Alonella nana, Chydrorus sphaericus, Alona affinis, A. quadrangularis, and Acroperus harpae. Postglacial pioneer species at Esrom were mainly Acroperus harpae and Chydrorus sphaericus; Alonella nana reached peak abundance during early phases in Esrom's history. The generalizations drawn from these observations are that the principal pioneer species of lakes are Chydrorus sphaericus, Alonella nana, Alona affinis, Acroperus harpae, and Alona quadrangularis. Furthermore, Alonella nana is consistently the most important chydorid species in those lakes with low nutrients (Blelham Tarn and Grane Langsø). Present-day distributions of this species in Denmark (Section I) have shown this species to be more prevalent in nutrient-poor waters. With the exception of Alonella nana, all pioneer species are fairly cosmopolitan. If, as Quade (1969) suggests, chydorid species are associated with floristic groups, the consistency of these pioneer species may be related to initial aquatic succession during early lake history.

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