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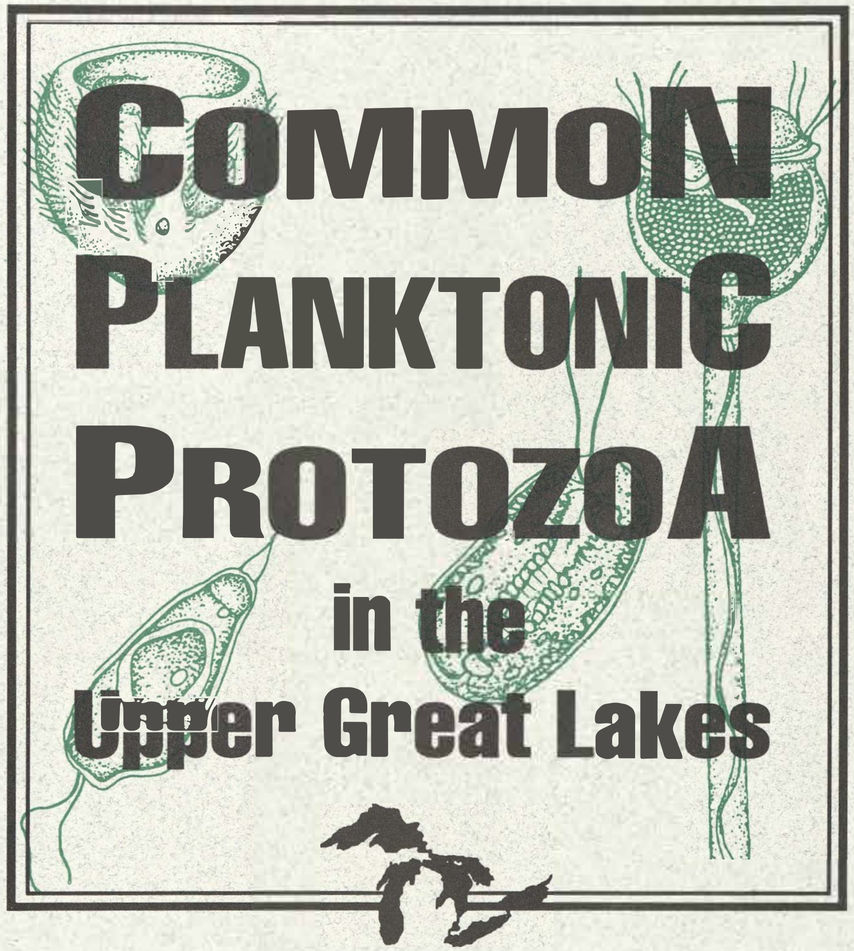
Common Planktonic Protozoa in the Upper Great Lakes



An Illustrated Guide

Hunter J. Carrick

Gary L. Fahnenstiel

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SUMMARY

This guide provides a body of taxonomic and ecological information about the planktonic protozoa that commonly occur in the upper Great Lakes (Lakes Huron, Michigan, and Superior). Our observations are based on more than 70 field collections obtained over a 10-year period (1979-1989) from offshore locations in these lakes using techniques readily available to most ecologists (light and epifluorescence microscopy). A separate taxonomic profile for each of 35 common protozoan taxa encountered is presented. The analysis is organized around six general aspects of each organism's ecology that include: taxonomic position, morphological description, distribution, a brief list of pertinent references, general comments (and observations), and a micrograph of the organism. Moreover, dichotomous keys to common protozoan orders and individual taxa are presented. We conclude that planktonic protozoa are an important component of the plankton in these lakes and, thus, need to be accounted in future studies. While this guide is not intended as a definitive taxonomic work, it is a holistic compilation of data that should prove valuable to those interested in freshwater, planktonic protozoa.

INTRODUCTION

The quantitative importance of protozoa in aquatic systems has not been realized until recently (Sherr and Sherr, 1984). The abundance, biomass, and seasonal dynamics of protozoan populations in both marine (e.g., Sorokin, 1977; Davis and Sieburth, 1982; Sherr et al., 1984), and to a lesser extent, freshwater (Beaver and Crisman, 1982; Pace, 1982; Pick and Caron, 1987; Taylor and Heynen, 1987; Nagata, 1988) systems, suggests that protozoan biomass rivals that of traditionally larger (> 200 µm in size) zooplankton (Taylor and Heynen, 1987; Carrick and Fahnenstiel, 1990). High growth and production rates for protozoa (e.g., Sherr et al., 1984; Nagata, 1988) indicate that these organisms may consume a greater percentage of microbial production (bacteria and < 20–µm phytoplankton) compared with larger zooplankton (e.g., Verity, 1986). Protozoa also play an important role as remineralizers of nutrients by virtue of their high grazing rates on bacteria and small algae (Goldman et al., 1985; Anderson et al., 1986).

In the Great Lakes, the quantitative importance of heterotrophic (Scavia et al., 1986; Scavia and Laird, 1987) and phototrophic (Caron et al., 1985; Fahnenstiel et al., 1986; Pick and Caron, 1987; Fahnenstiel and Carrick, 1992) picoplankton has been demonstrated. Higher bacterial production compared with primary production (annual averages) in Lake Michigan lends credence to the idea that ecosystem dynamics are largely governed by a detrital food web (Scavia, 1988). Protozoan production in Lake Michigan is comparable with bacteria (Carrick et al., 1992) and can account for the constancy in bacterial abundances (Scavia and Laird, 1987). While some data exist on the distribution and composition of protozoa in the Great Lakes (Pick and Caron, 1987; Taylor and Heynen, 1987; Carrick and Fahnenstiel, 1989, 1990), no working guide to their taxonomy and ecology presently exists.

SCOPE AND OBJECTIVES OF THE GUIDE

The systematics of the Protozoa can be contradictory and complicated by the combination of techniques (live observation, light microscopy, silver impregnation, and electron microscopy) sometimes required to achieve alpha-level taxonomy (Foissner, 1991). Such techniques are analytically laborious and require very specialized training to cross-correlate the structures identified by each. Moreover, no single method is optimal for the identification of all protists nor are many methods readily applicable to the analysis of natural samples. For instance, electron microscopy is usually performed on single species cultures, and live observation of organisms may not be feasible when large numbers of samples are collected.

Given these challenges, it is our primary intent here to offer a simple, yet comprehensive, illustrated guide to planktonic protozoa that occur in the upper Great Lakes (Lakes Huron, Michigan, and Superior). Our analysis was not restricted to a subset of the protozoa; the entire community was analyzed, including both heterotrophic and phototrophic forms of varying size (2–200 µm). Information regarding the taxonomy and ecology of the 35 most common (>5% abundance on at least one occasion) taxa is presented. Observations are based on more than 70 field collections obtained over a 10–year period (1979–1989) from offshore locations. All identifications were made using conventional microscopic techniques (light and epifluorescence). In this way, the guide is intended to be useful to a broad range of individuals conducting ecological research on the protozoa.

The strength of our approach lies in its simplicity and broad application to those with limited training in protozoology. In some situations, not all diagnostic characters necessary for good species-level description are revealed using conventional microscopy. The flagellated protists studied here were accurately categorized by body morphology, chromatophore structure, and flagellation type. Ciliated forms were identified to the generic level with confidence by cell body morphology, body ciliature, some internal structures, and description of the aboral zone of membranelles (AZM) (where cilia that are organized into compound rows are situated around the oral region of the cell). However, some subgeneric determinations require description of kinetid structure using electron microscopy and silver impregnation. Also, live observations can provide additional diagnostics such as swimming behavior, internal structure, morphogenic relations, and size estimates prior to preservation. We made subgeneric determinations by gross morphology of distinct and consistent groups that we were able to identify, and, thus, indicate their uniqueness by assigning them a species number.

Our analysis is organized around six general aspects of each organism's ecology, which are described in more detail below: taxonomic position, morphological description, distribution, a brief list of pertinent references, general comments (and observations), and a micrograph of the organism. The taxonomy used herein conforms to that outlined by Lee et al. (1985), although we acknowledge and discuss recent revisions to specific taxonomic groups. We have adopted this classification scheme, because of its completeness and the recognition it has received from the Society of Protozoologists. Second, information on the general cell morphology, size (average and range), and visible subcellular structures are discussed. Third, a brief synopsis of the each organism's distribution is given, highlighting the range in cell numbers observed from our sampling, with notes on their occurrence. For future reference, temporal and spatial water column organization in the lakes were defined by physical, chemical, and biological information collected simultaneously with water samples used to determine protozoan abundances (see methods). Fourth, one to several references that provide additional information about the taxon or genus (due to the paucity of information on individual protozoan species) are listed, including the page number where that individual is depicted in the reference. Fifth, any general comments pertaining to the taxon are discussed, such as preservation artifacts, occurrence of endosymbionts, trophic observations, or features used to distinguish it from similar taxa. Sixth, a photomicrograph of each taxon is provided.

METHODOLOGY

Sample Collection and Enumeration

Sampling was conducted in the three upper Great Lakes (Huron, Michigan, Superior) at single offshore stations during 1979–1989. In general, water was collected from 1 to 6 depths with a clean 5–liter or 30–liter PVC Niskin bottle usually at sundown (2000–2200 h). In Lake Huron (43° 56' N, 82° 21' W; depth=80 m), samples were collected on 30 occasions from 1986 to 1988 from surface (5 m) and subsurface (20–40 m) regions of the water column. Lake Michigan (43° 1' N, 86° 36' W; depth=100 m) was sampled on 21 dates from 1987 to 1989. Sampling in Lake Superior (47° 27' N, 88° 34' W; depth=230 m) was conducted on 20 dates during 1979–1983. Samples in both Lakes Michigan and Huron were collected at 5 m during the winter to early spring period (single samples January–April),

Table 1.--The taxonomic position (Order, Taxon) of 35 common planktonic flagellated protozoa (Sarcomastigophora) and ciliated protozoa (Ciliophora) observed in the upper Great Lakes. Where present (X), absent (-), and not sampled (?).

Taxonomic Position	Great Lake: Huron	Michigan	Superior
Phylum Sarcomastigophora			
Order Choanoflagellida			
Desmarella sp.	X	X	X
Order Chrysomonadida			
Chromulina sp.1	X	X	X
Chromulina minima	X	X	X
Ochromonas nana	X	X	X
Ochromonas ovalis	X	X	X
Dinobryon divergens	X	X	X
Order Cryptomonadida			
Cryptaulax sp.1	X	X	X
Cryptomonas erosa	X	X	X
Cryptomonas ovata	X	X	X
Cryptomonas ovata var. reflexa	X	X	X
Katablepharis ovalis	X	X	X
Rhodomonas lens	X	X	X
Rhodomonas minuta	X	X	X
Order Dinoflagellida			
Ceratium hirudinella	X	X	X
Gymnodinium helveticum	X	X	X
Gymnodinium varians	X	X	X
Peridinium inconspicuum	X	X	X
Order Prymnesiida			
Chrysochromulina parva	X	X	X
Phylum Ciliophora			
Order Choreotrichida			
Codonella cratera	X	X	?
Strobilidium sp.1	X	X	?
Strobilidium velox	X	X	?
Tintinnidium sp.1	X	X	?
Order Oligotrichida			
Pelagohalteria sp.1	X	X	?
Strombidium sp.1	X	X	?
Pelagostrombidium sp.1	X	X	?
Order Haptorida			
Askenasia sp.2	X	X	?
Lagynophyra sp.	X	X	?
Mesodinium sp.	X	X	?
Monodinium sp.2	X	X	?
Order Prorodontida			
Pseudobalanion sp.	X	X	?
Urotricha sp.1	X	X	?
Coleps sp.2	-	X	?
Order Sessilida			
Vaginacola sp.	X	X	?
Vorticella sp.1	X	X	?
Vorticella campanula	-	X	?

while more intensive sampling was conducted from May to November, a period when the water column temperature usually varied with depth. At least two samples were taken from each of the major thermal regions (epi-, meta-, and hypolimnia) as described by Wetzel (1983). During this sampling period, temperature profiles were measured with an electronic bathythermograph, and chlorophyll concentrations were determined fluorometrically (Strickland and Parsons, 1972).

On all sampling dates, the abundances of flagellated protozoa were determined from lake water samples transferred into 250-mL amber bottles and preserved with 0.3% acid Lugol's iodine. However, from 1987 onward, two separate water samples were collected in both Lakes Huron and Michigan. One sample was fixed with 1% Lugol's acid iodine (ciliate and microflagellate sample) while the second was fixed with 1% glutaraldehyde buffered with 0.1M sodium cacodylate (nanoflagellate sample). This was done because of the wide range in cell size, fragility, and abundance among the protozoa. The abundance of microflagellates (composed entirely of Dinoflagellida) and ciliates (Ciliophora, most >20- and <200-µm in size) were determined separately from nanoflagellates (Chloromonadida, Chrysomonadida, Cryptomonadida, and Choanoflagellida >2- and <20-µm in size). The potential trophic status of nanoflagellates was distinguished by the presence (phototrophic, Pnano) or absence (heterotrophic, Hnano) of pigmentation. The occurrence of chlorophyll bodies inside ciliates was common for several taxa, and was noted.

Nanoflagellates were enumerated using epifluorescent microscopy from slides prepared within 24 h of sampling. Subsamples (10–20 mL) were filtered onto prestained (irgalan black) 0.8-µm pore size Nuclepore filters and stained with primulin (Caron, 1983). The filters were then mounted between a microscope slide and coverslip with immersion oil. Prepared slides were immediately stored at -20°C and counted within 1 month to minimize the fading of fluorescence. Biomass was estimated by enumerating 400–500 individuals from each prepared slide using a Jena Lumar Microscope (mag. 1200x) equipped for autofluorescence (450–490 excitation and >515 emission), and primulin analysis (320–380 excitation and >420 emission).

The abundance and community composition of microflagellate and ciliate protozoa were determined using the Utermohl technique (Utermohl, 1958). Subsamples (25–50 mL) were settled onto coverslips for 24 h. The coverslips were then systematically scanned, whereby 400–1000 individuals were enumerated using a Wild M40 inverted microscope (magnification 250x).

Cell volumes were calculated for each taxon by measuring the cellular dimensions of at least 10 cells on at least 4 dates in each lake and applying appropriate geometric forms that best describe their shape (e.g., spheres, cones, cylinders). For the Ciliophora, these estimates were first converted to biomass (wet weight), assuming a specific weight of 1.0 $g \cdot mL^{-1}$, and subsequently converted to carbon, assuming 0.279 wet/dry conversion (Gates, 1984). Cellular volume estimates for the phototrophic flagellates (Chrysomonadida, Cryptomonadida, Dinoflagellida, Prymnesiida) were converted to carbon based upon Strathmann (1967) conversion factors, while cell volumes for heterotrophic flagellates (Choanoflagellida, Chrysomonadida, Cryptomonadida) were converted to carbon using the conversion factor 0.15 $g\ C \cdot mL^{-1}$ (Laws et al., 1984). In all cases, biomass estimates were not corrected for cell shrinkage due to preservation (Borsheim and Bratbak, 1987; Choi and Stoecker, 1989).

Ambient Water Column Conditions

Surface water temperatures during the 10 years of study ranged from 2.5° to 26°C. The timing of thermal stratification was relatively similar between lakes. Surface waters warmed from May to June and were maximal (15–26°C) in July–August. Following the scheme of Fahnenstiel and Scavia (1987a), we defined three major thermal periods for future reference: isothermal mixing (temp. <4.0°C, December–May sampling); intermediate stratification (temp. 4.0–15.0°C, June and October to November); and mid-stratification (temp. >15°C, July–September). In addition, a subsurface chlorophyll layer developed in the metalimnia of these lakes. This appears to be a consistent structural and functional limnological characteristic in the upper Great Lakes (see Fahnenstiel and Scavia, 1987c) and will be referred to throughout the text that follows.

IDENTIFICATION KEY TO THE COMMON PROTOZOAN ORDERS OCCURRING IN THE UPPER GREAT LAKES

1. Cells bearing flagella (Sarcomastigophora) 2
1. Cells bearing cilia (Ciliophora) 8
2. Cells with single, apical flagellum 3
2. Cells bearing 2 or more flagella 4
3. Single or colonial colorless cells, apical microvilli network form funnel-like apical collar .... **Choanoflagellida**
3. Cells with scales, in a lorica, or naked; if pigmented, present as 2-4 parietal chromatophores .... **Chrysomonadida**
4. Flagella of equal length 5
4. Flagella of unequal length 6
5. Flagella inserted apically; if pigmented, bearing single cup-shaped chloroplast .... **Chloromonadida**
5. Flagella inserted subapically in oral furrow .... **Cryptomonadida**
6. Flagella inserted subapically 7
6. Flagella reside in transverse and longitudinal furrows; if pigmented, present as numerous discoid chromatophores .... **Dinoflagellida**
7. Flagella subapical in oral furrow; if pigmented,bearing single parietal chloroplast .... **Cryptomonadida**
7. Cells with scales, in a lorica, or naked; if pigmented, present as 2-4 parietal chromatophores .... **Chrysomonadida**
8. Body (somatic) ciliature reduced or absent 9
8. Body ciliature prominent 10
9. Aboral zone of membranelles forms a complete ring; cells either naked or loricate .... **Choreotrichida**
9. Aboral zone of membranelles forms an incomplete ring; cells are naked .... **Oligotrichida**
10. Body ciliature of one type 11
10. Body ciliature of two types 12
11. Body ciliature reduced to sub-equatorial fringe; most sessile, solitary or colonial, naked or loricate .... **Sessilida**
12. Body ciliature forms an apical brosse or band occupying upper 3/4 of cell, some armored .... **Prorodontida**
12. Apical or subapical cytosome (mouth) with a tubular passage extending inward to cytoplasm; body shape and ciliature variable .... **Haptorida**

IDENTIFICATION KEY TO THE COMMON PROTOZOAN TAXA OCCURRING IN THE UPPER GREAT LAKES

1. Cells bearing flagella (Sarcomastigophora) 2
1. Cells bearing cilia (Ciliophora) 18
2. Cells with single, apical flagellum 3
2. Cells bearing 2 or more flagella 5
3. Single or colonial colorless cells (5–6 by 3–4 µm), apical network of microvilli form funnel-like apical collar .... *Desmarella* **sp.1**
3. Cells with scales, in a lorica, or naked; if pigmented, 2 to 4 parietal chromatophores 4
4. Single spherical cells, diameter 2-3 µm, flagellum 2-4x body .... ***Chromulina* sp.1**
4. Single oviform cells, 3-4 long x 2-3 µm in breadth .... ***C. minima***
5. Apical flagella of equal or unequal length 6
5. Subapical flagella of unequal length 9
6. Cells colorless and free-swimming 7
6. Cells pigmented with two lateral chromatophores 8
7. Single colorless cells, spherical to oviform in shape; diameter 2-3 µm .... ***Ochromonas nana***
7. Single, colorless ovate cells, tapering to an apical point; 6-8 long by 5-8 µm in breadth .... ***O. ovalis***
8. Ovoid to ellipsoid cell encased in a lorica, lorica flexed at base and undulate at margins, cells unite to form dendritic colonies .... ***Dinobryon divergens***
8. Single naked cells with two lateral chromatophores, dorsiventrally flattened, posterior haptonema many times longer than body .... ***Chrysochromulina parva***
9. Subapical flagella inserted in oral furrow 10
9. Flagella attached in transverse and longitudinal furrows; if pigmented, bearing discoid chromatophores 15
10. Cells colorless 11
10. Cells pigmented 12
11. Longitudinal furrow conspicuous, solitary ellipsoid cells with lateral compression, anterior pointed, 10-20 µm long .... ***Cryptaulax* sp.1**
11. Ovate to ellipsoid cells with rounded anterior and posterior ends, conspicuous apical vacuole .... ***Katablepharis ovalis***
12. Cells large >15 µm with two chloroplast 13
12. Cells usually <15 µm bearing single chloroplast with one pyrenoid 14
13. Ovoid cell shape, length:breadth ratio >1.5 to <2x .... ***Cryptomonas ovata***
13. Ellipsoid to ovoid, length:breadth ratio >2x .... ***C. erosa***
13. Ellipsoid cells recurved at posterior end, length:breadth ratio >2x .... ***C. erosa v. reflexa***

IDENTIFICATION KEY TO THE COMMON PROTOZOAN TAXA OCCURRING IN THE UPPER GREAT LAKES (Continued)

14. Ovoid cells with rounded anterior, dorsally curved comma shape, large posterior refractive body .... ***Rhodomonas minuta***
14. Ovoid to oviform cells, tapers to point on both ends .... ***R. lens***
15. Cells armored bearing conspicuous plates 16
15. Cells naked without plates 17
16. Large cells of irregular shape (>150 µm), 2 or more arm-like projections... ***Ceratium hirudinella***
16. Small ovoid cells (<20 µm), strong dorsiventral asymmetry .... ***Peridinium inconspicuum***
17. Ovoid cells, slight dorsiventral asymmetry .... ***Gymnodinium varians***
17. Fusiform cells with pointed ends .... ***G. helveticum***
18. Somatic (body) ciliature highly reduced or absent 19
18 Body ciliature conspicuous 24
19. Adoral membranelles form complete ring; cells either naked or loricate..... 20
19. Adoral membranelles form incomplete ring; all cells naked 23
20. Cells present in lorica 21
20. Cells occur without a lorica 22
21. Bell-shaped to spherical cell body inside mineral vase-shaped lorica collared with reticulate rings .... ***Codonella cratera***
21. Cylindrical cells tapering to posterior, agglomerate, mineral lorica resembling a tube .... ***Tintinnidium* sp.1.**
22. Small spherical cells (10–16 µm) .... ***Strobilidium* sp.1**
22. Large bell-shaped cell (30–40 µm), posterior end tapers to a point .... ***S. velox***
23. Spherical cells (13–23 µm) bearing lateral bristles, endosymbionts usually present .... ***Pelagohalteria* sp.1**
23. Heart-shaped cells (31 x 24 µm) with slight somatic spiral, thin paratene cap about the posterior .... ***Strombidium* sp.1**
23. Cells ovoid to obovoid (40 x 33 µm) with slight somatic spiral, paratene cap with polysaccharide plaques encase entire posterior of cells .... ***Pelagostrombidium* sp.1**
24. Body ciliature of one type 25
24. Body ciliature of one or two types, cells with raised cytosome region 28
25. Body ciliature reduced to sub-equatorial fringe; cells sessile, solitary or colonial, naked or loricate 26
25. Body ciliature forming an apical band, cells ovoid or barrel-shaped, some armored 27
26. Ovoid cells (10–20 µm), solitary or gregarious, often attached to phytoplankton by a retractable stalk .... ***Vorticella* sp.1**

IDENTIFICATION KEY TO THE COMMON PROTOZOAN TAXA OCCURRING IN THE UPPER GREAT LAKES (Continued)

26. Bell-shaped cells (20–30 µm) solitary or gregarious, often attached to phytoplankton by a retractable stalk .... ***V. campanula***

26. Bell-shaped cells (15–20 µm) occurring in cup-shaped lorica (without stalk), solitary or gregarious, often attached to phytoplankton ...... ***Vaginacola* sp.**

27. Obovoid to cordiform cells with flattened apical cytosome (10–20 µm by 10–13 µm), body ciliature arranged as circumferential band surrounding the oral region, single caudal cilium .... ***Pseudobalanion* sp.**

27. Obovoid to cordiform cells, with oval apical cytosome (13–29 µm by 10–23 µm), body ciliature distributed even over upper 3/4 of cell body, single caudal cilium .... ***Urotricha* sp.1**

27. Barrel-shaped cells (39–56 µm by 26–39 µm), longitudinal armor-like plates with lateral teeth, oval apical cytosome, ciliature evenly distributed over cell body, single caudal cilium.. ***Coleps* sp.2**

28. Cilia arranged in conspicuous girdles 29

28. Cell flask-shaped, apex of cell body with distinct ventral bend .... ***Lagynophyra* sp.**

29. One circumferential ciliary girdle behind anterior oral dome, (cell body 18–26 µm long by 18–23 µm in breadth) .... ***Monodinium* sp.2**

29. Two circumferential ciliary girdles behind anterior oral dome, one extending forward .... ***Mesodinium* sp.**

29. Two circumferential ciliary girdles, one at cell equator, a second dense band of short cilia around oral region, cell body (13-23 µm long by 10–23 µm in breadth) .... ***Askenasia* sp.2**

TAXONOMIC PROFILES

Phylum: Sarcomastigophora
Order: Choanoflagellida

The choanoflagellates (or collared flagellates) are a morphologically distinct group that are of great ecological significance in a variety of aquatic habitats (Fenchel, 1987). Members of the group were originally considered plant-like protistians and were classified as a subclass or order in the Chrysophyta (see Bourrelly, 1968, 1970). Presently, most regard choanoflagellates as zooflagellates due to their lack of pigmentation, and, thus, group them in their own order in the class Zoomastigophorea (e.g., Leadbeater, 1985; Anderson, 1988). Taxonomic affinities within the order are based upon the ultrastructural characteristics of the periplast and colonial arrangement of cells (see Leadbeater, 1985).

Generally, choanoflagellates are free-living, colorless cells that occur singularly or arranged in colonies. Each cell bears a single apical flagellum around which a network of microvilli constitutes a funnel-like structure or collar. The nature of the periplast covering the cells varies among families within the order; species can be naked, bear sheath-like thecal cell coverings, or be encased in silicious lorica.

Members belonging to the Choanoflagellida occur in the upper Great Lakes, but are generally represented in low numbers (Carrick and Fahnenstiel, 1989). Because of this, we will present a taxonomic profile for a single taxon. A second rare taxon belonging to this group is not presented here (*Desmarella* sp.). This taxon occurs in colonies of 4–8 cells during initial thermal stratification.

Phylum: Sarcomastigophora
Order: Choanoflagellida
Taxon: *Desmarella* sp. 1

Description: Individuals usually occur in pairs or groups of four, but are sometimes solitary cells (Plate I, Figure 1). Cells are spherical or ovoid and bear sheath-like structures. The sheath is seen as a number of microvilli that extend from the cell body approximately the distance of the cell's diameter. The cell body bears a single apical flagellum. Cells range in size from 5 to 6 µm in length and 3 to 5 µm in breadth (average dimensions 6 x 4 µm).

Distribution: This taxon was present in low numbers in a number of samples we analyzed from all three upper Great Lakes. It achieved its greatest biomass in the surface waters during mid-stratification (range 50 to 200 cells mL^{-1}).

References:
Starmach, K. 1985. *Susswasserflora von Mittleeuropa*. Band I: Chrysophyceae und Haptophyceae. Gustav Fischer Verlag, Stuttgart, Deutschland (p. 43; Fig. 17).

Comments: Analysis with epifluoresent microscopy provides some advantages over traditional light microscopy techniques, given the fragile nature of these cells. Use of fluorescent stains enhances one's ability to resolve fine microvilli structure. Definitive taxonomic placement of this organism must be tempered, because exact structure of the lorica and collar is difficult to resolve without electron microscopy.

Phylum: Sarcomastigophora
Order: Chrysomonadida

The Chrysomonads are a diverse group of organisms that is well represented in the upper Great Lakes. This group has undergone a number of revisions in classification. Original classification schemes are presented by several investigators (e.g., Christensen, 1962; Bold and Wynne, 1978), which have since been updated based upon detailed ultrastructural information (e.g., Pienaar, 1980; Bold and Wynne, 1985; Hibberd and Leesdale, 1985). Both colorless and pigmented representatives of this group are abundant in the Great Lakes (e.g., Munawar and Munawar, 1975; Fahnenstiel and Scavia, 1987b; Carrick and Fahnenstiel, 1989).

In terms of general diagnostic characteristics, members belonging to this division can be flagellated (with single or bi-flagellation) or non-flagellated. For the purposes of this discussion, we will focus on the flagellated forms, as they are the most abundant Chrysomonads in the upper Great Lakes. These organisms have cells that bear a single flagellum or two flagella of unequal length inserted apically into the cell body. The long flagella (or single flagellum) usually bear bilateral tubular mastigonemes, while the second short flagellum (vestigial) is smooth. Cells are spherical, oval, or oblong in shape. Chrysomonads can be colorless or pigmented; pigmented forms commonly contain two (sometimes more) parietal chloroplasts (or chromophores) rich in chlorophylls *a*, *c* (*c1* and *c2*), and several carotenoids. The chloroplast may or may not have pyrenoid bodies. Some species possess an orange-red eyespot (stigma). The cell wall can be quite variable within this group; species can be naked, bear siliceous scales, exist in siliceous lorica, or be covered by mineralized body scales. Some species can produce cysts (statospores) composed of silica which can have ornamentation patterns that are species-specific and useful in making taxonomic determinations. Furthermore, the preservation of characteristic cell wall structures specific to many Chrysophytes makes these organisms useful paleolimnological markers (e.g., Smol, 1980).

Other taxa of members belonging to the Chrysomonadida occur in the upper Great Lakes, but were not as common (e.g., *Chrysolakas* sp., *Chrysosphaerella longispina*, *Diceras* sp., *Dinobryon bavaricum, Kephrion* sp., *Pseudokephrion* sp., *Mallomonas alpinus, M. pseudocoronata*, *Ochromonas globosa*, and *O. variablis*). For this reason we did not include an accompanying taxonomic profile for them, although their general distribution and autecology is discussed elsewhere (see Skuja, 1956, 1964).

Phylum: Sarcomastigophora
Order: Chrysomonadida
Taxon: *Chromulina* sp. 1

Description: Individuals of this taxon occur as single, spherical cells that are naked and lack any pigmentation (colorless). The cell body is smooth and bears a single apical flagellum that appears to be smooth and is greater than 2x the body diameter (Plate I, Figure 2). Cells are small, ranging in size from 2 to 3 µm in diameter (average size 2.5 µm).

Distribution: This taxon was present in all the samples we analyzed. It was abundant in most samples, but achieved its greatest biomass in surface waters during mid-stratification (range 500 to 4000 cells mL^{-1}).

References:

Huber-Pestalozzi, G. 1962. *Das phytoplankton des Susswassars*, 1. Halfte, Chrysophyceae farblose flagellaten heterokonten. E. Schweizerbart Verlag, Stuttgart (p. 28; Abb. 7).

Starmach, K. 1985. *Susswasserflora von Mittleeuropa*. Band I: Chrysophyceae und Haptophyceae. Gustav Fischer Verlag, Stuttgart, Deutschland (p. 43; Fig. 17).

Comments: We feel this taxon can only be enumerated accurately using epifluorescence microscopy due to its small size and lack of pigmentation. To our knowledge, this is one of the most abundant eukaryotic, planktonic organisms that occurs in the upper Great Lakes. We suspect that this taxon is a colorless form of *Chromulina parvula* Doflein, although its average flagellar length is greater. It is also similar in morphology to *C. elegans* Conrad, but without information about the chromophore structure utilized in original descriptions, it is difficult to make a definitive identification. This taxon is a very significant component of the pelagic food web because of its high growth (Carrick et al., 1992) and carbon flux rates to macrozooplankton (Carrick et al., 1991).

Phylum: Sarcomastigophora
Order: Chrysomonadida
Taxon: *Chromulina minima* Doflein

Description: This taxon is a single, naked, oviform cell that lacks any pigmentation (Plate I, Figure 3). The cell body bears a single apical flagellum (same length as cell body), which appears to be smooth. Cells are small, ranging in size from 3 to 4 µm in length and 2 to 3 µm in breadth (average 3 x 2 µm).

Distribution: This organism was present in all the samples we analyzed. It achieved its greatest biomass in the surface waters (upper 10 m) during mid-stratification (range 10 to 320 cells mL^{-1}). On average *C. minima* occurs in the water column at abundances of 50–100 cells mL^{-1}.

References:

Huber-Pestalozzi, G. 1962. *Das phytoplankton des Susswassars*, 1. Halfte, Chrysophyceae farblose flagellaten heterokonten. E. Schweizerbart Verlag, Stuttgart (p. 31; Abb. 15).

Starmach, K. 1985. *Susswasserflora von Mittleeuropa*. Band I: Chrysophyceae und Haptophyceae. Gustav Fischer Verlag, Stuttgart, Deutschland (p. 44; Fig. 26).

Comments: We feel this taxon can only be enumerated accurately using epifluorescence microscopy due to its small size and lack of pigmentation. We suspect that this taxon is a colorless form of *Chromulina minima*. It is differentiated from *Chromulina* sp.1 by its oviform cell shape.

Phylum: Sarcomastigophora
Order: Chrysomonadida
Taxon: *Ochromonas nana* Doflein

Description: Individuals consist of a single, spherical to oviform cell that appear to be naked (Plate I, Figure 4). The cell bears two smooth, apical flagella of unequal length. The primary flagellum is approximately equal to the cell diameter, while the secondary flagellum is 1/4 as long. The cell body is smooth, and internal organization is not easily discerned. Cells are small, ranging in size from 2 to 3 µm in diameter (average diameter 2.5).

Distribution: This taxon was well represented in all three lakes and occurred in nearly all samples we analyzed. Abundances range from 50 to 240 cells mL^{-1}, with maximal occurrence in the surface waters during summer thermal stratification (July–August). During late stratification, a bimodal distribution in cell density with depth can be observed.

References:

Huber-Pestalozzi, G. 1962. *Das phytoplankton des Susswassars*, 1. Halfte, Chrysophyceae farblose flagellaten heterokonten. E. Schweizerbart Verlag, Stuttgart (p. 166; Abb. 223A).

Starmach, K. 1985. *Susswasserflora vaon Mittleeuropa*. Band I: Chrysophyceae und Haptophyceae. Gustav Fischer Verlag, Stuttgart, Deutschland (p. 177; Fig. 341).

Comments: We believe this to be a colorless form of *Ochromonas nana*. Like the *Chromulina* taxa discussed above, epifluorescence microscopy may be required in order to enumerate this taxon with accuracy, owing to its small size and lack of pigmentation. However, it is admittedly difficult to distinguish this taxon from other specimens of close taxonomic affinity (e.g., *O. sphagnalis*) due to the restricted information on internal cellular structure and the fact that original descriptions are largely based upon the shape and location of chromatophores.

Phylum: Sarcomastigophora
Order: Chrysomonadida
Taxon: *Ochromonas ovalis* Doflein

Description: Cells of this taxon are generally spherical to ovate, tapering to an apical point (Plate I, Figure 5). The outer cell surface is smooth with several conspicuous vacuoles. Cells are of moderate size, being 6–8 µm in length and 5–8 µm in width (average 7 x 6 µm). Two smooth flagella of unequal length arise from the pointed apical region. The primary flagellum is 2–3x the cell length, while the secondary flagellum is equal in length.

Distribution: This taxon did not occur in all of our samples. It ranged in abundance from 7 to 231 cells mL^{-1} and achieved its greater numbers in deeper waters during mid- to late-stratification (August–November). Common cell densities for this taxon are 30–50 cells mL^{-1}.

References:

Huber-Pestalozzi, G. 1962. *Das phytoplankton des Susswassars*, 1. Halfte, Chrysophyceae farblose flagellaten heterokonten. E. Schweizerbart Verlag, Stuttgart (p. 167; Abb. 222).

Starmach, K. 1985. *Susswasserflora von Mittleeuropa*. Band I: Chrysophyceae und Haptophyceae. Gustav Fischer Verlag, Stuttgart, Deutschland (p. 179; Fig. 350).

Comments: This taxon is one of the larger heterotrophic flagellates encountered in the upper Great Lakes. Epifluorescence microscopy may be required for identification due to its delicate cell structure and lack of pigmentation. The abundance of food vacuoles inside the cells suggests that this species is an active grazer.

Phylum: Sarcomastigophora
Order: Chrysomonadida
Taxon: *Dinobryon divergens* Imhof

Description: Cells of this taxon are ovoid to ellipsoid and are generally encased in a lorica. Two smooth flagella of unequal length arise from the apical region. The primary flagellum is 1/2 the cell length. Lorica are flexed near the base, and the lateral margins may be irregular or undulate. Lorica are companulate, being united into multi-branched, free-swimming colonies (Plate I, Figure 6). Cells are of moderate size from 6 to 8 µm in length and 5 to 8 µm in width (average 7 x 6 µm).

Distribution: This organism was a minor component of the plankton (<5 cells mL^{-1}). However, on occasion it achieved high densities in the deep chlorophyll region (400–500 cells mL^{-1}).

References:

Huber-Pestalozzi, G. 1962. *Das phytoplankton des Susswassars*, 1. Halfte, Chrysophyceae farblose flagellaten heterokonten. E. Schweizerbart Verlag, Stuttgart (p. 167; Abb. 222).

Starmach, K. 1985. *Susswasserflora von Mittleeuropa.* Band I: Chrysophyceae und Haptophyceae. Gustav Fischer Verlag, Stuttgart, Deutschland (p. 179; Fig. 350).

Comments: Several species of *Dinobryon* exist in the upper Great Lakes. These include *D. bavaricum*, *D. sertularia*, and *D. sociale*. *D. divergens* is the most common and is distinguished by the diverging nature of the branching colonies.

Phylum: Sarcomastigophora
Order: Cryptomonadida

The Cryptomonads are well represented in a number of aquatic environments, but despite their obvious importance, the taxonomy of this group is poorly described. For example, one of the most abundant Cryptomonads, *Rhodomonas minuta*, has been referred to as *Cryptomonas curvata* (Gyseva, 1936), *Cryptomonas pusilla* (Anton and Duthie, 1981), *Rhodomonas lacustris* (Javornicky, 1976), and *Chroomonas pusilla* (Happey-Wood, 1976). This group has undergone revision in classification from original schemes presented elsewhere (e.g., Skuja, 1956; Javornicky, 1974). Updated taxonomy is largely based upon ultrastructural information (e.g., Hibberd and Leesdale, 1985) or analyses of population size and shape (Anton and Duthie, 1981).

Members belonging to this group are generally ovoid, oval, or oblong shaped unicells that are dorsi-ventrally flattened (asymmetric); palmelliod stages do exist. Cells are generally biflagellated, with flagella of equal or unequal length and usually bearing bilateral tubular mastigonemes. The flagella are inserted subapically into an oral furrow (gullet), which in turn is lined with ejectosomes (similar to trichocysts). Also unique to the group is the cell covering (periplast) that is best described as a trilaminate plasmalemma that covers internal plating (Bold and Wynne, 1985). Cryptomonads can be colorless, but if pigmented, commonly contain one or two parietal chloroplasts rich in chlorophylls *a*, *c*, phycobilin proteins, carotenoids (*a* and ß), and xanthophylls. The chloroplast usually contains one large pyrenoid body central to the cell body. Some species possess an orange-red eyespot.

Both colorless and pigmented representatives of this group are abundant in the Great Lakes (e.g., Munawar and Munawar, 1975; Fahnenstiel and Scavia, 1987b; Carrick and Fahnenstiel, 1989). In addition, a number of other Cryptomonads that exist in the upper Great Lakes were not included here due to their infrequent occurrence. Some of these include *Chroomonas acuta*, *Cryptomonas marssonii*, *C. brevis*, *C. reflexa*, and *C. rostratiformis*.

Phylum: Sarcomastigophora
Order: Cryptomonadida
Taxon: *Cryptaulax* sp.1

Description: Cells are ellipsoid to oblong (slipper-shaped) with a prominent subapical furrow and devoid of pigment (colorless) (Plate II, Figure 7). The furrow gives rise to two subapical flagella of unequal length (a swimming flagella and trailing flagella). The longer flagella is 1.5–2x greater in length than the short flagella. The range in cell size is from 6 to 12 μm long by 4 to 6 μm wide (average 8 x 5 μm).

Distribution: This species was sporadically represented in our samples; abundance of the taxon ranged from 4 to 58 cell mL^{-1}. Maximal abundances were achieved in the surface waters (<10 m depth) usually during mid-stratification (July to August).

References:
Skuja, H. 1956. Grundzuge der algenflora und algenvegetation der Fjeldgegenden um abisko in Schwedisch-Lappland. *Nova Acta Reg. Soc. Sci. Upsal.* Ser. IV Vol. 16 No. 3 (p. 351; Taf. LXI, Fig. 1--4).

Comments: This taxon is one of the larger colorless flagellates in the upper Great Lakes. It appears to resemble *C. rhomboidea* Skuja *or C. concoidea* Skuja. It is readily distinguished from *Katablepharis ovalis* Skuja by virtue of its slipper-shaped cell body and the prominent furrow. Unlike *K. ovalis*, *Cryptaulax* lacks an apical storage body, and its flagella appear to be inserted at a more subapical orientation along the cell body.

Phylum: Sarcomastigophora

Order: Cryptomonadida

Taxon: *Cryptomonas erosa* Ehrenberg

Description: These cells are ellipsoid to ovoid in shape with no curvature of the cell (Plate II, Figure 8). The anterior end is distinctly beveled with margination at the gullet. The posterior end is narrowly rounded. Two subapical flagella of unequal length are present. The gullet can approach the middle of the cell, and two marginal chromatophores are present. This taxon has a length to breadth ratio of approximately two. The range in size of these cells is from 16 to 47 µm long by 10 to 21 µm wide (average 27 x 13 µm).

Distribution: Generally, this is the most abundant *Cryptomonas* species observed in all three upper Great Lakes. Cell densities range from 6 to 160 cells mL^{-1} with maximum occurrence during mid-stratification, usually in the region of the deep chlorophyll layer.

References:

Anton, A. and H. C. Duthie. 1981. Use of cluster analysis in the systematics of the algal genus *Cryptomonas*. *Canadian Journal of Botany* 59:992–1002.

Comments: This taxon is easily viewed with light microscopy. Despite its relatively low abundance throughout the year, it can contribute significantly to phototrophic biomass by virtue of its large cell size.

Phylum: Sarcomastigophora

Order: Cryptomonadida

Taxon: *Cryptomonas erosa* var. reflexa Marsson

Description: These cells are similar in size and shape to *C. erosa* except that the posterior end is curved (Plate II, Figure 9). Two subapical flagella of unequal length are present. Refractory bodies are usually distinct in this variety. The range in size of these cells is from 20 to 36 µm long by 8 to 6 µm wide (average 26 x 12 µm).

Distribution: This taxon is generally less abundant than *C. erosa.* Abundance ranged from 0 to 30 cells mL^{-1} with maximal densities being realized during intermediate thermal stratification (May–June and October–November).

References:

Anton, A. and H. C. Duthie. 1981. Use of cluster analysis in the systematics of the algal genus *Cryptomonas. Canadian Journal of Botany* 59:992–1002.

Comment: This taxon has not been universally recognized as a distinct variety of *C. erosa*. We have included it herein, because it appears to be a distinct morphotype. Again, this taxon is of sufficient cell size to be viewed adequately with light microscopy and is quantitatively important at times.

Phylum: Sarcomastigophora

Order: Cryptomonadida

Taxon: *Cryptomonas ovata* Ehrenberg

Description: These cells are ovoid to obovoid with an obliquely truncated anterior end and distinct margination at the anterior end (Plate II, Figure 10). The posterior end is rounded. Two subapical flagella of unequal length are present, and two large marginal chromatophores are conspicuous. The length to breadth ratio of these cells is approximately 1.6. The range in cell size of the taxon is from 16 to 34 µm long by 7 to 9 µm wide (average 23 x 14 µm).

Distribution: Abundances range from 7 to 80 cells mL^{-1}. This organism is most abundant during isothermal mixing periods and intermediate thermal stratification (May–June and October–November).

References:

Anton, A. and H. C. Duthie. 1981. Use of cluster analysis in the systematics of the algal genus *Cryptomonas*. *Canadian Journal of Botany* 59:992–1002.

Comments: This taxon is easily distinguished with the light microscope from other *Cryptomonas* taxa by its oval cell shape, which is not flexed or tapered.

Phylum: Sarcomastigophora
Order: Cryptomonadida
Taxon: *Katablepharis ovalis* Skuja

Description: Cells of this taxon are colorless (non-pigmented) and ovate to oblong in shape with rounded ends. Two flagella of unequal length are present (Plate II, Figure 11). The longer flagella is 1.5–2x greater in length than the shorter flagellum. Cells usually possess an oval vacuole located near the posterior end of the cell. Contractile vacuoles and the remnants of ingested cells within these vacuoles are commonly observed. Cell size ranges from 6 to 12 µm in length by 4 to 6 µm in width (average 8 x 5 µm).

Distribution: This was the most abundant heterotrophic cryptomonad found in upper Great Lakes; abundances ranged from 5 to 509 cells mL^{-1}. Maximal abundances were achieved during mid-stratification (July–August) in the vicinity of the upper deep chlorophyll region.

References:
Skuja, H. 1956. Grundzuge der algenflora und algenvegetation der Fjeldgegenden um abisko in Schwedisch-Lappland. *Nova Acta Reg. Soc. Sci. Upsal.* Ser. IV Vol 16 No. 3 (p. 350; Taf. LXI, Fig. 1–4).

Comments: *K. ovalis* is one of the largest colorless flagellates in the upper Great Lakes. We suspect this taxon to be an active algivore. It has autofluorescent remnants in its contractile vacuoles rich in phycobilin proteins. Its distribution overlaps with phototrophic picocyanobacteria and cryptomonads and its growth potential is high (approaching two doublings per day in the summer, Carrick et al., 1992). It is grazed by macro-zooplankton (Carrick et al., 1991) and, thus, we feel this indicates its significance to food web dynamics in Lake Michigan.

Phylum: Sarcomastigophora

Order: Cryptomonadida

Taxon: *Rhodomonas lens* Pascher & Ruttner

Description: Cells are ovoid with equally narrowed and cuspidate anterior and posterior ends (Plate II, Figure 12). Cells may be slightly curved when viewed from the side. A posterior clear tip may be present, but this tip is substantially smaller than the one present in *R. minuta*. Two subapical flagella of unequal length are present. A single prominent pyrenoid can be seen in most specimens. These cells are slightly larger than *R. minuta* (next), ranging from 10 to 17 µm in length by 6 to 9 µm in breath (average 12 x 8 µm).

Distribution: *R. lens* is an important component of the upper Great Lakes protozoan community. This taxon was generally less abundant than *R. minuta*, except perhaps during isothermal mixing periods. Cell densities range from 3 to 100 cells mL^{-1}. Maximal abundance was found during isothermal mixing periods and intermediate thermal stratification.

References:

Happy-Wood C. M. 1976. Vertical migration patterns in phytoplankton of mixed species composition. *Br. Phycol. J.* 11:355–369.

Javornicky, R. 1976. Minute species of the genus *Rhodomonas* Karsten (Cryptophyceae). *Arch. Protistenk.* 118:98–106.

Willen, E., M. Oke, and F. Gonzalez. 1980. *Rhodomonas minuta* and *Rhodomonas lens* (Cryptophyceae)—Aspects on form-variation and ecology in Lakes Malaren and Vattern, Central Sweden. *Acta Phytogeographica Suecica* 68: 163-172.

Comments: Organisms of this morphotype have been identified as *Cryptomonas pusilla* (Anton and Duthie, 1981) and *Chroomonas pusilla* (Happy-Wood, 1976). Javornicky (1976) has even suggested that *R. lens* and *R. minuta* should be called *R. lacustris*. Hopefully, this confusion will be reconciled in the near future; however, until it is, we continue to recognize this complex as two distinct morphotypes, *R. minuta* and *R. lens*, for the reasons discussed herein and outlined in Willen et al. (1980).

Phylum: Sarcomastigophora
Order: Cryptomonadida
Taxon: *Rhodomonas minuta* Skuja

Description: Cells are curved (comma-shaped) and ovoid to pyriform when viewed from the side (Plate II, Figure 13). The anterior end is broadly rounded, while the posterior end is very narrow and pointed. A relatively large refractory body ("leucosin") is located at the posterior end. Two subapical flagella of unequal length are present. One large chromatophore bearing a large, prominent pyrenoid body are found in all cells. A furrow and two rows of trichocysts can be seen in some specimens. The range in size of the species is from 5 to 14 µm long by 3 to 8 µm wide (average 9 x 5 µm).

Distribution: *R. minuta* is one of the most abundant protozoans found in all three upper Great Lakes with abundances ranging from 30 to 1300 cells mL^{-1}. Maximal abundance in all three lakes occurred during the mid-stratification period in the region of the deep chlorophyll layer (Fahnenstiel and Glime, 1980; Fahnenstiel and Scavia, 1987). Most typically, R. *minuta* abundances are approximately 100 cells mL^{-1}.

References:
Lund, J. W. G. 1962. A rarely recorded but very common British alga, *Rhodomonas minuta* Skuja. *Br. Phycol. Bull.* 2:133–139.
Willen, E., M. Oke, and F. Gonzalez. 1980. *Rhodomonas minuta* and *Rhodomonas lens* (Cryptophyceae)- Aspects on form-variation and ecology in Lakes Malaren and Vattern, Central Sweden. *Acta Phytogeogr. Suec.* 68:163–172.

Comments: This taxon is easily recognizable and is a common protozoan in many freshwater aquatic systems. There is some taxonomic uncertainty regarding this morphotype, as it has been called *R. lacustris* (Javornicky, 1976). The size of the clear posterior end appears to be correlated with growth rate or physiological condition; very actively growing cells usually have very small storage areas. This taxon also appears to be very sensitive to containment in experimental bottles.

Phylum: Sarcomastigophora

Order: Dinoflagellida

The dinoflagellates (armored flagellates) are a morphologically diverse group of biflagellated unicells that occur in aquatic ecosystems worldwide. These organisms are particularly prolific in marine ecosystems where, at times, they are capable of forming large toxic blooms. Freshwater dinoflagellate blooms that adversely affect fish populations have also been observed (Burkholder et al., 1992). In terms of their taxonomic position, phycologists classify these organisms in their own phylum (Pyrrophyta, Prescott, 1968), while protozoologists give the group ordinal status in the class Phytomastigophorea (Lee et al., 1985).

Dinoflagellates have vegetative cells that either bear flagella or are flagellated at one point in their life history. In most taxa, one flattened flagellum is housed in a transverse furrow (cingulum) and a second posterior, acronematic flagellum is attached within a longitudinal groove, normally on the ventral cell surface (sulcus). A smaller, less diverse group of dinoflagellates has cells bearing two anterior flagella. The flagella of both groups are usually smooth. Moreover, the relative positioning of the cingulum and sulcus and the detailed cell wall plating are species-specific characteristics and, therefore, useful in making species-level determinations.

Cells can be spherical, ovoid, or irregularly shaped and bearing two to four arm-like projections that are often dorsally flattened and flexed. The outer covering of dinoflagellates is composed of several membrane layers (theca), within which the cell membrane is included. Armored species have additional outer layering of structural cellulose and polysaccharides, while unarmored species are covered with a membrane complex (naked). Most commonly, cells contain numerous discoid chloroplasts (or chromophores) rich in chlorophylls *a*, *c*, ß-carotene, and a number of xanthophylls now known to be specific to this group (e.g., peridinin, neoperidinin). The common storage product is starch. Some species have an eyespot but this characteristic is by no means widely shared within the group. Members of this order also possess some very unique attributes such as the production of neurotoxins, bioluminescence, and protection by a variety of structures (i.e., trichocysts, nematocysts).

Some representatives of this group are abundant in the Great Lakes and constitute a significant fraction of plankton biomass (e.g., Munawar and Munawar, 1975; Carrick and Fahnenstiel, 1990). In this section we profile four of the most abundant dinoflagellates encountered in water samples collected from the upper Great Lakes. Several less abundant taxa also occur but will not be dealt with here (e.g., *Peridinium wisconsinense*, *Gymnodinium ordinatum*, *G. uberrimum,* and *Cystodinium* sp.).

Phylum: Sarcomastigophora

Order: Dinoflagellida

Taxon: *Ceratium hirudinella* (O.F.Muell.) Dujardin

Description: *Ceratium* is an irregularly-shaped, armored dinoflagellate (Plate III, Figure 14). The cell body is dorsiventrally flattened bearing from 1 to 3 (usually 3) posterior arms and a single anterior arm (all approximately 50–80 µm in length). This taxon is biflagellated in the vegetative state; one flagellum is situated in a transverse sulcus, and a second trails at the posterior end of the cell from a central, longitudinal cingulum. *Ceratium* is one of the largest protozoan taxa we have encountered in our samples, ranging in size from 130 to 228 µm in length and 51 to 68 µm in breadth (average 60 x 185 µm). Discoid chromatophores are dispersed throughout the cell.

Distribution: The density of *Ceratium* exhibited strong seasonality. It was absent from the water column during the winter to spring period and became evident only during mid-stratification (range from 0.1 to 3.0 cells mL^{-1}). Following this period, it again became scarce. The distribution of this taxon was usually restricted to the upper 15 m of the water column.

References:

Prescott, G.W. 1973. *Algae of the Western Great Lakes Area*. 5th Ed., WM. C. Brown, Dubuque, Iowa (p. 437; Plate 92, Figs 4–5).

Huber-Pestalozzi, G. 1968. *Das phytoplankton des Susswassars*. Band XVI, 3. Teil, Cryptophyceae, Chloromonadophyceae, Dinophyceae. E. Schweizerbart Verlag, Stuttgart (p. 260; Abb. 276).

Comments: Despite its large size, this taxon is capable of relatively high growth rates and appears to be resistant to grazing by macrozooplankton (Carrick et al., 1991).

Phylum: Sarcomastigophora
Order: Dinoflagellida
Taxon: *Gymnodinium helveticum* Penard

Description: *G. helveticum* is fusiform in shape with both the anterior and posterior of the cell tapering to a point (Plate III, Figure 15). Cells lack armoring (naked), and the hypopcone (lower half of cell) is approximately 1/3 of the cell volume. Chromatophores are abundant throughout, and cells are biflagellated. Cells range in size from 29 to 52 µm long by 16 to 29 µm wide (average dimensions 40 x 23 µm).

Distribution: *G. helveticum* maintains a presence throughout the year in all three lakes. Much of the variation in cell densities can be accounted for by changes in its vertical orientation. This taxon occurs throughout the isothermal water column during the winter-spring period (January–May). It achieves maximal abundances (4–6 cells mL^{-1}) once a thermocline develops (early June); as the thermocline deepens, a high density of cells accumulate in the vicinity of the deep chlorophyll layer (4–5 cells mL^{-1}). The species is still present during late stratification (October–November), but as in the spring isothermal period, it is more evenly distributed with depth.

References:

Huber-Pestalozzi, G. 1968. *Das phytoplankton des Susswassars.* Band XVI, 3. Teil, Cryptophyceae, Chloromonadophyceae, Dinophyceae. E. Schweizerbart Verlag, Stuttgart (p. 139; Abb. 121–122).

Skuja, H. 1948. *Taxonomie des Phytoplankton Einiger Seen in Uppland, Schweden.* Symbolae Botanicae Upsalienses IX:3 (p. 369; Taf. XXXVIII, Figs. 38–41).

Comments: This taxon is similar to, yet distinguishable from, *G. fuscum* by the presence of the anterior point in the cell body, while the latter has a rounded anterior. Our data agree with previous observations for the taxon that indicate its mixotrophic capabilities (Frey and Stoermer, 1980). *G. helveticum* is capable of phagocytizing cells of a size comparable to its own, such as diatoms. The percent of cells containing ingested prey tends to increase with depth in Lake Michigan (H.J. Carrick, unpubl. data). Hence, we feel this taxon may be an important grazer of the spring diatom bloom as well as components of the deep chlorophyll layer during summer.

Phylum: Sarcomastigophora
Order: Dinoflagellida
Taxon: *Gymnodinium varians* Maskell

Description: Cells of *G. varians* are ovoid with a slight asymmetry (Plate III, Figure 16). The anterior of the cell is rounded, while the posterior slopes to a gentle point. Cells lack armoring (naked), and the hypopcone is approximately equal in size to the epicone. Chromatophores are abundant throughout, giving the cell a dark appearance. Cells range in size from 10 to 16 μm long by 7 to 16 μm wide (average dimensions 13 x 11 μm).

Distribution: *G. varians* tended to be most abundant at cooler water temperatures (<15°C). During spring isothermal periods, it can be abundant throughout the water column (0–2 cells mL^{-1}). During early to mid-stratification (June–July), the greatest numbers occurred at depths of 20–30 m in the water column (1–2 cells mL^{-1}) in the region of the deep chlorophyll layer. By late stratification, low numbers were again distributed throughout the water column.

References:

Huber-Pestalozzi, G. 1968. *Das phytoplankton des Susswassars.* Band XVI, 3. Teil, Cryptophyceae, Chloromonadophyceae, Dinophyceae. E. Schweizerbart Verlag, Stuttgart (p. 136; Abb. 115).

Comments: While this taxon is readily observed with light microscopy, it can be overlooked due its small size and fine cell structures that can be masked with standard Lugol's preservation (1% final conc.). Examination with epifluorescent microscopy shows that pigmentation within these cells can be sparse, suggesting that this taxon may be mixotrophic. This observation requires further study for confirmation.

Phylum: Sarcomastigophora
Order: Dinoflagellida
Taxon: *Peridinium inconspicuum* Lemmermann

Description: Cells are small and ovoid in shape (Plate III, Figure 17). The apical region draws to a gentle point, while the posterior is rounded and bears 2–3 short horns. There is a slight dorsiventral flattening to the cells, and this can be seen when cells are viewed from the poles. The transverse furrow is broad and divides the cell body into a large epicone and smaller hypocone. The longitudinal furrow occupies the hypocone and extends a short distance into the epicone. Chromatophores appear to be abundant throughout, giving the cell a dark appearance. Cells range in size from 16 to 23 µm long by 16 to 20 µm wide (average dimensions 25 x 22 µm).

Distribution: *P. inconspicuum* occurred in most of the samples we analyzed (range 0.02–2.5 cells mL^{-1}). It achieved greatest abundance in the surface waters during mid-stratification (July–September, water temperatures >15 ^{o}C).

References:
Prescott, G.W. 1973. *Algae of the Western Great Lakes Area*. Wm. C. Brown, Dubuque, Iowa (p. 433; Plate 90, Figs. 22–24).

Comments: As with *G. varians*, this taxon can be overlooked during routine light microscopy enumeration at 200x magnification; hence, the conspecific name. While this taxon is capable of high growth rates, no obvious seasonal pattern in growth was noted (Carrick et al., 1992).

Phylum: Sarcomastigophora
Order: Prymnesiida

The prymnesimonads (or haptophytes) are a group of unicellular protists, whose vegetative cells are flagellated or who have flagellated developmental stages produced during some portion of their life history. Originally, this group was considered a family in the Chrysophyceae (e.g., Pascher, 1918; Smith, 1950). More recently, these organisms have been placed into a separate division as denoted herein (e.g., Hibberd, 1980; Hibberd and Leesdale, 1985).

These organisms have cells that bear two flagella of equal or unequal length. The flagella are usually smooth. A filiform organelle called a haptonema is also present and differs in both form and function from the flagella (for discussion, see Hibberd and Leesdale, 1985). While the function of the haptonema is debatable, it is generally thought to aid in locomotion or in capturing prey, thus giving these organisms mixotrophic capabilities. This organelle can be quite long relative to the cell's length or barely recognizable (vestidule) and is carried either coiled or straight. The point of attachment of the haptonema to the cell varies among species, as a variety of arrangements have been observed. Cells are spherical, oval, or flattened and flexed giving the appearance of a saddle. Most commonly, cells contain two parietal chloroplasts (or chromophores) rich in chlorophylls *a*, *c* (*c1* and *c2*), and several carotenoids (Bold and Wynne, 1985). Some species have an eyespot, but this characteristic is by no means widely shared within the group.

The major representative of this group is *Chrysochromulina parva* Lackey which is presented herein. This taxa is very abundant in the Great Lakes and constitutes a significant fraction of the plankton biomass (e.g., Munawar and Munawar, 1975; Carrick and Fahnenstiel, 1989). Other more rare prynesiomonads have been observed in our samples, but have yet to be adequately identified.

Phylum: Sarcomastigophora

Order: Prymnesiida

Taxon: *Chrysochromulina parva* Lackey

Description: This taxon is characterized as a naked free-swimming unicell (Plate III, Figure 18). The cell body is dorsiventrally flattened, thus resembling a saddle and appearing almost discoid in front view. The cell possesses two flagella of unequal length and a haptonema that is many times greater than the cell's length (3–10x). Two lateral (or marginal) chromatophores are readily observed. Cell size ranges from 3 to 7 µm in length by 2 to 4 µm in width (average dimensions 5 x 3 µm).

Distribution: This taxon was abundant in nearly all samples and constitutes a substantial fraction of the phototrophic plankton biomass in all three of the upper Great Lakes (Munawar and Munawar, 1975; Carrick and Fahnenstiel, 1989). A large range in the seasonal cell density of this taxon was observed (range 130 to 2800 cells mL^{-1}). Greatest abundances were achieved during early thermal stratification (June–July) in the vicinity of the upper deep chlorophyll layer.

References:

Hibberd, D.J. and G.F. Leesdale. 1985. Order 7. Pymnesiida. In *Illustrated guide to the Protozoa.*, J.J. Lee, S.H. Hutner, and E.C. Bovee (eds.). Soc. of Protozool. Lawrence Kansas (p. 76; Fig. 1).

Smith, G.M. 1950. *The Freshwater Algae of the United States.* McGraw-Hill, New York (p. 425; Fig. 339).

Starmach, K. 1985. *Susswasserflora von Mittleeuropa.* Band I: Chrysophyceae und Haptophyceae. Gustav Fischer Verlag, Stuttgart, Deutschland (p. 468; Fig. 1016).

Comments: This is a very abundant organism and an important component of the pelagic food web in the upper Great Lakes. It is capable of high growth rates and is readily grazed on by crustacean zooplankton (Carrick et al., 1991, 1992). Use of epifluorescence microscopy appears to enhance one's ability to accurately enumerate this taxon, due to its small size and delicate structure. We suspect this taxon is mixotrophic because it has been observed to ingest fluorescently labeled bacteria (H.J. Carrick, unpubl. data). This might, in part, account for the general decrease in cell size and pigmentation in surface populations that occurs following thermal stratification.

Phylum: Ciliophora
Order: Choreotrichida

Ciliates belonging to this order are common faunal components of the plankton in a variety of aquatic ecosystems (e.g., Beaver and Crisman, 1989). Original taxonomic work has included this group in the order Oligotrichida (Corliss, 1979; Curds et al., 1983). Small and Lynn (1985) have erected a new subclass (Choreotrichia) that contains two orders: Choreotrichida and Oligotrichida. Some original descriptions of choreotrichous ciliates may need to be reevaluated due to the detection of additional diagnostic features revealed with silver impregnation (Lynn and Montagnes, 1988). Similarities in the morphogenesis of nominal choreotrichous (strobiliids) and oligotrichous (strombiliids) ciliates provides a basis for placing these orders in one subclass, Oligotrichia, and discarding the Choreotrichia (Petz and Foissner, 1992). We have adopted Small and Lynn's (1985) classification scheme herein for consistency, thereby treating the group at the ordinal level more remotely related to members of the Oligotrichida.

The body form of choreotrichous ciliates is ovoid to elongate, bell shaped, or cylindrical with reduced somatic (body) ciliature. The order includes both loricate and naked species. Buccal (oral) cilia are conspicuous and well-defined, and appear as an aboral zone of membranelles to form a complete circle. Some species may be raptorial, most are planktonic suspension feeders.

Ciliates of this order are well represented in the Great Lakes (Taylor and Heynen, 1987; Carrick and Fahnenstiel, 1990). While we present detailed information on four taxa, a number of other forms were observed during the course of this study. They include one unidentified species of *Strobilidium* that is delineated from the two presented herein by cell body shape and size (average size 25 x 22 µm), and a second, larger species of *Tintinnidium* that remains to be classified (size 49 x 19 µm).

Phylum: Ciliophora
Order: Choreotrichida
Taxon: *Codonella cratera* Leidy

Description: Cells are encased in an agglomerate of mineral particles that forms a vase-shaped lorica ranging in size from 55 to 68 µm long and 39 to 46 µm wide. The lorica is collared with reticulate rings and flared at the opening. The cell body is bell-shaped to spherical (size range 33–22 µm) with an aboral zone of membranelles that forms a complete apical ring (Plate IV, Figure 19).

Distribution: The taxon is abundant in the surface waters of both Lakes Huron and Michigan during spring mixing to early stratification (April–June) with cell densities ranging from 200 to 1000 cells L^{-1}. Following thermal stratification, *Codonella* was abundant in the deep chlorophyll region (depth 20–40 m). On one occasion (18 June 1989) this taxon achieved extremely high densities (>5,000 cells L^{-1}), and many cells were observed undergoing sexual reproduction.

Reference:

Corliss, J.O. 1979. *The Ciliated Protozoa: Characterization, Classification and Guide to the Literature.* 2nd Ed. Pergamon Press. London (p. 303; Plate XXXI 25,26,35–37).

Curds, C.R., M.A. Gates, and D. McL. Roberts. 1983. *British and Other Freshwater Ciliated Protozoa.* Part II. Cambridge Univ. Press, Cambridge, England (p.362; Fig. 213).

Foissner, W., and N. Wilbert. 1979. Morphologie, infraciliatur und Okologie der limnischen Tintinnina: *Tintinnidium fluviatile* Stein, *Tintinnidium pusillum* Entz, *Tintinnopsis cylindrata* Daday und *Codonella cratera* (Leidy) (Ciliophora, Polyhymenophora). *Journal of Protozoology* 26: 90–103.

Small, E.B. and D.H. Lynn. 1985. Phylum Ciliophora. In *Illustrated Guide to the Protozoa.*, J.J. Lee, S.H. Hutner, and E.C. Bovee (eds.). Society of Protozoology, Lawrence, KS (p. 441; Fig. 3).

Comments: Cell bodies may appear spherical following preservation with Lugol's iodine. The distribution of this taxon coincides with the spring diatom bloom. Its subsequent occurrence in the deep chlorophyll layer of Lakes Huron and Michigan suggests that it may be seeded by sedimentation from surface populations. Thus, we suspect this taxon grazes on diatoms and other components of the spring bloom in the upper Great Lakes. Information for Lake Superior does not exist at present.

Phylum: Ciliophora

Order: Choreotrichida

Taxon: *Strobilidium* sp.1

Description: Cells are subspherical and range in size from 10 to 16 μm in diameter (average 13 μm). They bear an aboral zone of membranelles that forms a complete circle. This taxon also displays some somatic curvature, although not as conspicuously as other taxa belonging to this genus (Plate IV, Figure 20). However, it is unclear at present whether the somatic ciliature of this taxon spiral at the posterior pole, making it a true member of the genus *Strobilidium* (Petz and Foissner, 1992).

Distribution: *Strobilidium* sp.1 was the most abundant ciliate encountered in this study. It occurred in nearly all the samples we analyzed from both Lakes Huron and Michigan (from 500 to 4,320 cells L^{-1}). This taxon became numerically dominant during mid-stratification (July), achieving abundances greater than 4,000 cells L^{-1} in both lakes. The occurrence of this taxon was greatest in the euphotic zone during the summer and more specifically in the upper 10 m of the water column.

Reference:

Corliss, J.O. 1979. *The Ciliated Protozoa: Characterization, Classification and Guide to the Literature.* 2nd Ed. Pergamon Press. London (p. 302; Plate XXXI 14,15).

Curds, C.R., M.A. Gates, and D. McL. Roberts. 1983. *British and Other Freshwater Ciliated Protozoa.* Part II. Cambridge Univ. Press, Cambridge, England (p. 356; Fig. 210).

Small, E.B. and D.H. Lynn. 1985. Phylum Ciliophora. In *Illustrated Guide to the Protozoa*, J.J. Lee, S.H. Hutner, and E.C. Bovee (eds.). Society of Protozoology, Lawrence, KS (p. 447; Fig. 36).

Comments: This taxon exhibits the highest growth rates of any protozoan for which we have estimates (max. rate > 2 day^{-1}, Carrick et al., 1992). Given the size of this taxon, it most likely feeds on picoplankton-sized cells (Fenchel, 1987). Preliminary estimates of grazing by *Strobilidium* sp.1 indicate this to be true (Fahnenstiel et al., 1991). Thus, it is not surprising that its peak abundance coincides with maximal abundances of bacteria (Scavia and Laird, 1987) and picocyanobacteria (Fahnenstiel and Carrick, 1992) in Lake Michigan.

Phylum: Ciliophora
Order: Choreotrichida
Taxon: *Strobilidium velox* Faure-Fremiet

Description: These large conical or bell-shaped cells range in size from 30 to 40 μm in diameter and usually taper to a posterior point (average size 40 μm long and 35 μm wide). Cells bear an aboral zone of membranelles that form a complete circle (Plate IV, Figure 21). This taxon has strongly somatic curvature, often with somatic cilia being grouped into recognizable bundles (Grim, 1987). Recent analyses suggest that this taxon be moved to the new genus *Rimostrombidium* because, unlike other Strobiliids, it does not have somatic cilia that spiral at the posterior pole of the cell body (Petz and Foissner, 1992).

Distribution: While this taxon was not numerically dominant in many of our samples (from 40 to 220 cells L^{-1}), *Strobilidium velox* constituted a large fraction of total ciliate biomass on several dates owing to its large cellular volume. Generally, *S. velox* was abundant in winter and spring samples and declined thereafter in both lakes. Following thermal stratification, this taxon maintained moderate standing stocks in the vicinity of the deep chlorophyll layer (depth 20–40 m).

References:

Corliss, J.O. 1979. *The Ciliated Protozoa: Characterization, Classification and Guide to the Literature*. 2nd Ed. Pergamon Press. London (p. 302; Plate XXXI 14,15).

Curds, C.R., M.A. Gates, and D. McL. Roberts. 1983. *British and Other Freshwater Ciliated Protozoa*. Part II. Cambridge Univ. Press, Cambridge, England (p. 356; Fig. 210).

Grim, J.N. 1987. The kinetid structures of the Choreotrichous ciliate *Strobilidium velox* and an assessment of its evolutionary lineage. *Journal of Protozoology* 34: 117–123.

Small, E.B. and D.H. Lynn. 1985. Phylum Ciliophora. In *Illustrated Guide to the Protozoa*, J.J. Lee, S.H. Hutner, and E.C. Bovee (eds.). Society of Protozoology, Lawrence, KS (p. 447; Fig. 36).

Comments: In order to obtain accurate abundance estimates for this taxon, sedimentation of larger volumes of lake water may be required. Due to its large cell size, *S. velox* can be identified under lower magnification (mag. 50–100x).

Phylum: Ciliophora
Order: Choreotrichida
Taxon: *Tintinnidium* sp.1

Description: These cylindrical cells (range 16 to 26 µm length, 13 to 19 µm breadth) taper to a cone-shaped, often elongated posterior end (average size 22 x 15 µm). The posterior cell, is in turn attached to the inner wall of an agglomerate, tubular lorica, which is slightly larger than the encased cell. The lorica is unflared and without a collar, often giving the appearance of an unconsolidated matrix of mineral particles. The aboral zone of membranelles forms a closed apical circlet (Plate IV, Figure 22).

Distribution: This taxon demonstrated a great range in abundance throughout the study (range 20 to 1,350 cells L^{-1}). *Tintinnidium* was most abundant in both Lakes Huron and Michigan during spring mixing to early stratification (May–June) and declined in occurrence thereafter.

References:

Corliss, J.O. 1979. *The Ciliated Protozoa: Characterization, Classification and Guide to the Literature.* 2nd Ed. Pergamon Press. London (p. 303; Plate XXXI 17,18,28).

Curds, C.R., M.A. Gates, and D. McL. Roberts. 1983. *British and Other Freshwater Ciliated Protozoa.* Part II. Cambridge Univ. Press, Cambridge, England (p. 364; Fig. 214).

Foissner, W., and N. Wilbert. 1979. Morphologie, infraciliatur und Okologie der limnischen Tintinnina: *Tintinnidium fluviatile* Stein, *Tintinnidium pusillum* Entz, *Tintinnopsis cylindrata* Daday und *Codonella cratera*(Leidy) (Ciliophora, Polyhymenophora). *Journal of Protozoology* 26: 90–103.

Small, E.B. and D.H. Lynn. 1985. Phylum Ciliophora. In *Illustrated Guide to the Protozoa*, J.J. Lee, S.H. Hutner, and E.C. Bovee (eds.). Society of Protozoology, Lawrence, KS (p. 441; Fig. 1).

Comments: This taxon tends to co-occur with *Codonella* during the transition period between spring mixing and early thermal stratification. *Tintinnidium* sp. can be confused with a second similar taxon of larger size (average size 44.8 x 18.6 µm) that probably belongs to the same genus but is less abundant.

Phylum: Ciliophora
Order: Oligotrichida

Oligotrichous ciliates are common faunal components of the plankton in a variety of aquatic ecosystems. As mentioned previously, Small and Lynn (1985) have erected the subclass (Choreotrichia) that contains two orders (Choreotrichida and Oligotrichida). Thus, the number of taxa classified within the Oligotrichida has been reduced. For consistency, we have utilized the work of Small and Lynn (1985) and recognize the Oligotrichida as an order of classification housing two families; the Halteriidae and Strombidiidae. Some original descriptions of oligotrichous ciliates may need to be reevaluated due to the detection of additional diagnostic features revealed with silver impregnation and electron microscopy (Lynn et al., 1988). Furthermore, differences in the morphogenesis of oligotrichous ciliates provides some basis for elevating the Halteriidae to a separate order, because they appear to more closely related to Hypotrichs compared with the Oligotrichs (Petz and Foissner, 1992).

General body form is ovoid to bell-shaped with reduced somatic ciliature. All species are naked, bearing no lorica or external cell coverings although some species bear lateral bristles. The aboral zone of membranelles is conspicuous and well-defined, forming an incomplete circle. The first zone of membranelles is located inside the buccal cavity, while a second encircles much of the anterior pole of the cell. Some species may be raptorial, but most are planktonic suspension feeders.

Like the Choreotrichida, members of this order are well represented in the Great Lakes (Taylor and Heynen, 1987; Carrick and Fahnenstiel, 1990). While we present detailed information on three taxa, a number of other forms were observed during this study. They include one unidentified species of *Strombidium* sp.3 that is delineated from the two described herein by cell shape and size (average dimensions 56 x 42 μm), and a second larger, yet presently unidentified taxon probably belonging to the genus *Halteria* (diameter 18 μm).

Phylum: Ciliophora
Order: Oligotrichida
Taxon: *Pelagohalteria* sp.1

Description: *Pelagohalteria* sp.1 has spherical cells ranging in diameter from 13 to 23 µm (average 15.3 µm). An aboral zone of membranelles is evident, yet does not form a complete circle. Somatic cilia are present and occur with two pairs of lateral bristles (Plate V, Figure 23). Most individuals contain endosymbionts that occur as spherical green bodies approximately 1–3 µm in diameter.

Distribution: *Pelagohalteria* achieved its greatest abundance during the early to mid-thermal stratification period (June–July) in both Lakes Huron and Michigan. While this taxon was not consistently dominant, it was present in the majority of our samples at abundances ranging from 200 to 1,680 cells L^{-1}.

Reference:

Corliss, J.O. 1979. *The Ciliated Protozoa: Characterization, Classification, and Guide to the Literature.* 2nd Ed. Pergamon Press. London (p. 302; Plate XXXI 1–4).

Curds, C.R., M.A. Gates, and D. McL. Roberts. 1983. *British and Other Freshwater Ciliated Protozoa.* Part II. Cambridge Univ. Press, Cambridge, England (p. 346; Fig. 204).

Foissner, W., A. Skogstad, and J.R. Pratt. 1988. Morphology and infaciliature of *Trochiliopsis australis* N. Sp., *Pelagohalteria viridis* (Fromentel, 1876) N.G., N. Comb., and *Strobilidium lacustris* N.Sp. (Protozoa, Ciliophora). *Journal of Protozoology* 35: 489–497.

Small, E.B. and D.H. Lynn. 1985. Phylum Ciliophora. In *Illustrated Guide to the Protozoa*, J.J. Lee, S.H. Hutner, and E.C. Bovee (eds.). Society of Protozoology, Lawrence, KS (p. 447; Fig. 37).

Comments: We observed one other taxa of similar appearance that are delineated by size and shape and the absence of endosymbionts. This taxon appears to contain within it pigmented endosymbionts (Taylor and Heynen, 1987; Carrick and Fahnenstiel, 1990); their dark spherical bodies (ca. 1–3 µm diameter) are readily observable following preservation with Lugol's iodine. Moreover, this taxon has high growth potential (> 1.5 day^{-1}) and is likely to be an important bacterivore in the Great Lakes (Carrick et al., 1992).

Phylum: Ciliophora
Order: Oligotrichida
Taxon: *Strombidium* sp.1

Description: Cells are obovoid to heart-shaped and range in size from 26 to 39 µm in length and 23 to 26 µm in breadth (average size 31 x 24 µm). An open circlet of aboral membranelles is present; some somatic curvature results in slight spiraling. A circumferential paratene closes around the posterior of the cell, giving the appearance of a thin, cap-like covering (Plate V, Figure 24).

Distribution: *Strombidium* sp.1 was abundant in our samples (range 200 to 1240 cells L^{-1}). It accounted for a portion of the large increase in total ciliate abundance that occurred during the onset of thermal stratification (May–June) in both Lakes Huron and Michigan (Carrick and Fahnenstiel, 1990). However, its numbers decreased following thermal stratification and was present in lower numbers thereafter in the vicinity of the deep chlorophyll layer (depth 20–40 m).

References:

Corliss, J.O. 1979. *The Ciliated Protozoa: Characterization, Classification and Guide to the Literature*. 2nd Ed. Pergamon Press. London (p. 302; Plate XXXI 6–10).

Curds, C.R., M.A. Gates, and D. McL. Roberts. 1983. *British and Other Freshwater Ciliated Protozoa*. Part II. Cambridge Univ. Press, Cambridge, England (p. 360; Fig. 212).

Krainer, K.H. 1991. Contributions to the morphology, infaciliature and ecology of the planktonic ciliates *Strombidium pelagicum* n.sp., *Pelagostrombidium mirabile* (Penard, 1916) n.g. comb., and *Pelagostrombidium fallax* (Zacharias, 1896) n.g., n.comb. (Ciliophora, Oligotrichida). *Europ. J. Protozool.* 27: 60–70.

Small, E.B. and D.H. Lynn. 1985. Phylum Ciliophora. In *Illustrated Guide to the Protozoa*, J.J. Lee, S.H. Hutner, and E.C. Bovee (eds.). Society of Protozoology, Lawrence, KS. (p. 448; Fig. 40).

Comments: This taxon is distinguished from *Pelagostrombidium* sp.1 by its smaller cell size and less prominent posterior cap.

Phylum: Ciliophora
Order: Oligotrichida
Taxon: *Pelagostrombidium* sp.1

Description: Cells are ovoid to nearly globular, ranging in size from 32 to 65 μm in length and 20 to 48 μm in breadth (average size 41.4 x 33.2 μm). Open circlets of aboral membranelles with some somatic curvature. The peristomial collar at the anterior of the cell body has a broad buccal lip, giving the impression that membranelles extend outward from the interior. A circumferential paratene closes around the upper half of the cell body. Polysaccharide plaques cover the bottom 2/3 of the cell, giving the appearance of a rigid, lorica-like structure (Plate V, Figure 25).

Distribution: *Pelagostrombidium sp.1* was abundant in many of our samples (range 200 to 2000 cells L^{-1}). It accounts for much of the large increase in total ciliate abundance, which occurs during the onset of thermal stratification (May–June) in both Lakes Huron and Michigan (Carrick and Fahnenstiel, 1990). This taxon was a major component of a subsurface ciliate community that develops in the vacinity of the deep chlorophyll layer (depth 20–40 m) in both lakes during thermal stratification (June–August).

References:

Corliss, J.O. 1979. *The Ciliated Protozoa: Characterization, Classification and Guide to the Literature.* 2nd Ed. Pergamon Press. London (p. 302; Plate XXXI 6–10).

Curds, C.R., M.A. Gates, and D. McL. Roberts. 1983. *British and Other Freshwater Ciliated Protozoa.* Part II. Cambridge Univ. Press, Cambridge, England (p. 360; Fig. 212).

Krainer, K.H. 1991. Contributions to the morphology, infaciliature and ecology of the planktonic ciliates *Strombidium pelagicum* n.sp., *Pelagostrombidium mirabile* (Penard, 1916) n.g. comb., and *Pelagostrombidium fallax* (Zacharias, 1896) n.g., n.comb. (Ciliophora, Oligotrichida). *Europ. J. Protozool.* 27: 60–70.

Small, E.B. and D.H. Lynn. 1985. Phylum Ciliophora. In *Illustrated Guide to the Protozoa*, J.J. Lee, S.H. Hutner, and E.C. Bovee (eds.). Society of Protozoology, Lawrence, KS. (p. 448; Fig. 40).

Comments: Like *Halteria*, this taxon appears to contain pigmented endosymbionts that appear as spherical dark bodies (ca. 2–3 μm diameter) following preservation with Lugol's iodine. This taxon is similar to *Pelagostrombidium fallax* Zacharias as described by Krainer (1991).

Phylum: Ciliophora

Order: Haptorida

This order encompasses one of the more diverse groups of Ciliophora. Descriptions of the order given by Corliss (1979) and Curds (1982) are in general agreement. Both recognize the order as being composed of five common families (Enchelyidae, Spathidiidae, Tracheliidae, Didiniidae, and Actinobolonidae) with Corliss observing a sixth family (Protohalliidae) consisting of a single genus, *Protohallia*. Small and Lynn (1985) view things somewhat differently. They observe three orders common to those described above (Enchelyidae, Spathidiidae, and Didiniidae), but the family Tracheliidae has been restructured and is now referred to as Trachelophyllidae. Also, the genus *Lacrymaria* has been placed in its own family (Lacrymariidae). More pertinent to our work here, the genera *Askenasia*, *Mesodinium*, and *Myrionecta* have been moved from the family Didiniidae and placed into the Mesodiniidae, because they possess two types of body ciliature rather than one. In general, ciliates in this order appear to be raptorial carnivores common in both benthic and planktonic environments. A recent reanalysis of nominal species of *Askenasia* using silver impregnation has revealed several new species and a new genus, *Rhabdoaskenasia* (Krainer and Foissner, 1990). The establishment of *Rhabdoaskenasia* is based upon the occurrence of club-shaped extrusomes occurring along the cytopharynx extending inward from the mouth to the cytoplasm. Because this structure is not diagnostic of Haptorida, the new genus *Rhabdoaskenasia* has been transferred to the order Cyclotrichida.

With reference to microscopic identification, body shape is not a good diagnostic feature, and hence is not stressed in original descriptions of the order. The morphologic diversity that exists includes cells of ovoid to irregular shape with some bearing 1–3 arm-like projections. Classification is based primarily on four characteristics commonly shared by most taxa within the group: the existence of an apical or subapical cytosome (or mouth), a cytopharynx (non-ciliated tubular passage to the inner cytoplasm), which extends inward from the mouth and is not permanently eversible, the existence of clavate or sensory cilia, and an oral dome that is supported by sets of microtubules, along which, trichocysts may be present.

Members of this order are well represented in the Great Lakes (Taylor and Heynen, 1987; Carrick and Fahnenstiel, 1990) and cover three of the families mentioned above (Didiniidae, Mesodiniidae, and Tracheliidae). While we present detailed information on four taxa, other forms were observed during this study. These taxa include: a second smaller species of both *Askenasia* (average diameter 16 µm) and *Monodinium* (16 x 10 µm), and the rare occurrence of *Myrionecta* (39 x 33 µm) and *Spathidium* (45 x 30 µm).

Phylum: Ciliophora
Order: Haptorida
Taxon: *Askenasia* sp.2

Description: This taxon has obpyriform to pyramidal shaped cells that taper conically (often times to a sharp point) toward the anterior mouth or cytosome (Plate V, Figure 26). Body ciliature consists of two types: a tapering fan of cilia that proceeds from the anterior quarter of the cell forward (pectinelles), and an equatorial girdle (cirral) of longer cilia. Cells also bear a conspicuous mouth leading to a cytopharynx that extends inward and appears to be eversible. Size range for this taxon is from 13 to 23 μm long and 10 to 23 μm wide (average size 19 x 16 μm). Silver impregnation is needed to ascertain whether this taxon belongs to the genus *Askenasia* or *Rhabdoaskenasia*.

Distribution: This taxon occurs in both Lakes Huron and Michigan with abundances ranging from 40 to 800 cells L^{-1}. Peak densities were observed following thermal stratification and more specifically from July to August in the surface waters, when water temperatures were generally greater than 20°C.

References:

Corliss, J.O. 1979. *The Ciliated Protozoa: Characterization, Classification and Guide to the Literature*. 2nd Ed. Pergamon Press. London (p. 216; Plate XXII, Fig. 74).

Curds, C.R. 1982. *British and Other Freshwater Ciliated Protozoa.* Part I. Cambridge Univ. Press, Cambridge, England (p. 152; Fig. 99).

Krainer, K.H., and W. Foissner. 1990. Revision of the genus *Askenasia* Blochmann, 1895, with proposal of two new species and description of *Rhabdoaskenasia minima* N.G., N.Sp. (Ciliophora, Cyclotrichida). *Journal of Protozoology* 37: 414–427.

Small, E.B. and D.H. Lynn. 1985. Phylum Ciliophora. In *Illustrated Guide to the Protozoa*, J.J. Lee, S.H. Hutner, and E.C. Bovee (eds.). Society of Protozoology, Lawrence, KS. (p. 472; Fig. 23).

Comments: *Askenasia* most likely feeds raptorially on a variety of phytoplankton and other protozoa by virtue of its eversible cytopharynx.

Phylum: Ciliophora

Order: Haptorida

Taxon: *Lagynophyra* sp.

Description: Cells of this taxon are lanceolate to clavate with a ventrally reflexed anterior end (Plate V, Figure 27). An apical cytosome is present with an eversible cytopharynx; the oral region also appears to have clavate cilia and toxicysts. Cilia appear to organize longitudinally into a kinetodesmata. Size range for this taxon is from 33 to 46 µm long and 13 to 23 µm wide (average size 41 x 18 µm).

Distribution: While this taxon is numerically rare relative to other ciliates, it did account for a significant fraction of ciliate biomass on several occasions due to its large cellular volume. In both lakes, *Lagynophyra* ranged in density from 20 to 220 cells L^{-1} and was most common during the summer months.

Reference:

Corliss, J.O. 1979. *The Ciliated Protozoa: Characterization, Classification and Guide to the Literature.* 2nd Ed. Pergamon Press. London (p. 215; none).

Curds, C.R. 1982. *British and Other Freshwater Ciliated Protozoa.* Part I. Cambridge Univ. Press, Cambridge, England (p. 112; Fig. 65).

Small, E.B. and D.H. Lynn. 1985. Phylum Ciliophora. In *Illustrated Guide to the Protozoa*, J.J. Lee, S.H. Hutner, and E.C. Bovee (eds.). Society of Protozoology, Lawrence, KS. (p. 471; Fig. 18).

Comments: *Lagynophyra*, like *Askenasia* appears to feed raptorially on a variety of phytoplankton and other protozoa by virtue of its eversible cytopharynx. This is one of the larger, more rare protozoa observed in our samples, and for this reason, it is difficult to obtain accurate abundance estimates.

Phylum: Ciliophora
Order: Haptorida
Taxon: *Mesodinium* sp.

Description: Cells of this taxon are lanceolate in shape with a strongly tapering conical oral region (Plate V, Figure 28). An apical cytosome is present with an eversible cytopharynx; the oral region also appears to have clavate cilia (and toxicysts) with capitate tentacles. Cilia are organized into a single girdle, extending both to the anterior and posterior of the cell. Cells range in size from 10 to 23 µm in length and 13 to 29 µm in width (average size 22 x 14 µm).

Distribution: This taxon demonstrated much variation in its distribution (from 20 to 2,720 cells L^{-1}) in both Lakes Huron and Michigan. *Mesodinium* was sporadically represented in samples throughout the year, but it increased dramatically during late stratification. An autumn bloom of *Mesodinium* appeared to originate in the deep chlorophyll region in September 1987, leading to large standing stocks throughout the water column by late stratification.

Reference:
Corliss, J.O. 1979. *The Ciliated Protozoa: Characterization, Classification and Guide to the Literature.* 2nd Ed. Pergamon Press. London (p. 217; Plate XXII, Figs. 63,64).
Curds, C.R. 1982. *British and Other Freshwater Ciliated Protozoa.* Part I. Cambridge Univ. Press, Cambridge, England (p.158; Fig. 104).
Small, E.B. and D.H. Lynn. 1985. Phylum Ciliophora. In *Illustrated Guide to the Protozoa*, J.J. Lee, S.H. Hutner, and E.C. Bovee (eds.). Society of Protozoology, Lawrence, KS. (p. 472; Fig. 24).

Comments: Like the other members of this order that occur in the Great Lakes, *Mesodinium* also possesses an eversible cytopharynx and, therefore, most likely feeds raptorially on a variety of prey. This taxon became numerically dominant during late stratification in both 1988 and 1989. It achieved densities of bloom proportion in both years.

Phylum: Ciliophora
Order: Haptorida
Taxon: *Monodinium* sp.2

Description: Cells of this taxon are nearly spherical with a strongly conical oral region (Plate V, Figure 29). An apical cytosome is present with an eversible cytopharynx. The conical oral region also appears to have clavate cilia and toxicysts, as in the taxon *Mesodinium*. However, cilia are organized in a single circumferential band (or girdle) at the base of the conical oral area. Cells of this taxon range in size from 18 to 26 µm in length by 18 to 23 µm in breadth (average dimensions 24 x 20 µm).

Distribution: In both lakes, this taxon was usually a minor component of the ciliate community (from 20 to 220 cells L^{-1}). *Monodinium* was most abundant in the surface water (5–10 m) during mid-stratification.

Reference:

Corliss, J.O. 1979. *The Ciliated Protozoa: Characterization, Classification and Guide to the Literature*. 2nd Ed. Pergamon Press. London (p. 217; Plate XXII, Figs. 62).

Curds, C.R. 1982. *British and Other Freshwater Ciliated Protozoa.* Part I. Cambridge Univ. Press, Cambridge, England (p.160; Fig. 105).

Small, E.B. and D.H. Lynn. 1985. Phylum Ciliophora. In *Illustrated Guide to the Protozoa*, J.J. Lee, S.H. Hutner, and E.C. Bovee (eds.). Society of Protozoology, Lawrence, KS. (p. 472; Fig. 21).

Comments: Because *Monodinium* also possesses an eversible cytopharynx, we presume that this taxon feeds raptorially on a variety of prey like the other members of this order that occur in the Great Lakes. Based on its small size, it is likely a predator on small flagellates and phytoplankton. It is easily differentiated from a second taxon of *Monodinium* that is smaller and oblong or barrel-shaped (average dimensions 16 x 10 µm).

Phylum: Ciliophora
Order: Prorodontida

Representative species in the order Prorodontida are characterized as predacious ciliates that are largely planktonic and exist under a variety of water quality conditions. Corliss (1974) established the group as a suborder, and this convention is also recognized by Curds (1982). Both observe two families within the suborder (Prorodontidae and Colepidae). The suborder was raised to the ordinal level by Small and Lynn (1985), wherein they observe six families, two of which are common to the description above. Three of the six families described by Small and Lynn are pertinent to our work here: Balanionidae, Urotrichidae, and Colepidae. The genus *Balanion* has been placed in a family of its own (Balanionidae), while the Urotrichidae is newly formed and consists of three genera (including *Urotricha*). Lastly, the family Colepidae has been expanded to include three more genera in addition to *Coleps*, the only original member.

The cell body of prorodontids is generally ovoid to elliptical with flattening of the apical region in some species. The cytosome (or mouth) is apical or subapical and appears to be round or oval in form. Very characteristic is the brosse or dorsal brush of cilia, present as kinetid units of three or more files at the anterior end of the cell. Somatic trichocysts may also be present, and one genus has skeletal plates.

Members of this order occur in most samples collected from the Great Lakes (Taylor and Heynen, 1987; Carrick and Fahnenstiel, 1990). Taxonomic profiles of three taxa are presented herein; other forms were observed during this study. Some of these include a second larger species of both *Urotricha* (16 µm) further differentiated by its three caudal cilia, and smaller species of *Coleps* (16 x 10 µm).

Phylum: Ciliophora
Order: Prorodontida
Taxon: *Pseudobalanion* sp.

Description: Cells exhibit an obovoid to cordiform morphology with a flattened apical region that tapers posteriorly (Plate VI, Figure 30). The cytosome is apical and oval in shape. Body cilia are arranged as a dense circumferential anterior band (or girdle) surrounding the oral area and a single posterior cilium. This taxon is also quite small; cell size ranges from 10 to 20 μm long and 10 to 13 μm wide (average dimensions 15 x 11 μm).

Distribution: This taxon was generally absent in winter and spring samples (January–April). *Psuedobalanion sp.* was present following thermal stratification (June) and its numbers were maximal in the surface waters (range 20 to 600 cells L^{-1}).

Reference:

Muller, H. 1991. *Pseudobalanion planctonicum* (Ciliophora, Prostomatida): ecological significance of an algivorous nanociliate in a deep mesoeutrophic lake. *Journal of Plankton Research* 13:247–262.

Small, E.B. and D.H. Lynn. 1985. Phylum Ciliophora. In *Illustrated Guide to the Protozoa*, J.J. Lee, S.H. Hutner, and E.C. Bovee (eds.). Society of Protozoology, Lawrence, KS. (p. 463; Fig. 7).

Comments: This taxon is one of the smallest ciliates we encountered. It can be difficult to distinguish from *Urotricha* species. However, upon close examination at sufficient magnification (>250x), the existence of the anterior restriction of ciliature can be seen. The occurrence of this taxon has not been widely documented.

Phylum: Ciliophora
Order: Prorodontida
Taxon: *Urotricha* sp.1

Description: Cells exhibit an obovoid to cordiform morphology (Plate VI, Figure 31). The cytosome is apical and oval in shape. Cilia are evenly distributed on the upper 3/4 of the cell body, leaving the posterior bare with the exception of a single posterior cilium. This taxon is also quite small; cell size ranges from 13 to 29 µm in length by 10 to 23 µm in breadth (average dimensions 22 x 14 µm).

Distribution: This taxon occurred in all the samples we collected (from 200 to 4,040 cells L^{-1}). *Urotricha sp.* achieved its greatest abundance during early to mid-stratification (June–August). Its occurrence generally decreases with depth.

Reference:

Corliss, J.O. 1979. *The Ciliated Protozoa: Characterization, Classification and Guide to the Literature.* 2nd Ed. Pergamon Press. London (p. 214, Plate XXII, Figs. 25).

Curds, C. R. 1982. *British and Other Freshwater Ciliated Protozoa.* Part I. Cambridge Univ. Press, Cambridge, England (p. 96; Fig. 51).

Small, E.B. and D.H. Lynn. 1985. Phylum Ciliophora. In *Illustrated Guide to the Protozoa*, J.J. Lee, S.H. Hutner, and E.C. Bovee (eds.). Society of Protozoology, Lawrence, KS. (p. 464; Fig. 9).

Comments: This taxon is abundant, exhibits high growth potential (Carrick et al., 1992), and is heavily preyed upon by crustacean zooplankton (Carrick et al., 1991). Thus, it is likely to play a key trophic role in the upper Great Lakes. This taxon can be confused with a second *Urotricha* species observed in our samples. The second species has three posterior cilia and is generally larger in size (average size 28 x 10 µm).

Phylum: Ciliophora
Order: Prorodontida
Taxon: *Coleps* sp.2

Description: The body is barrel-shaped and bears armored (skeletal) plates with lateral teeth, all of which are arranged in longitudinal rows (Plate VI, Figure 32). The cytosome is apical and oval in shape. Cilia are evenly distributed over the cell body; a single caudal cilium is also present. This taxon is large with cells ranging in size from 39 to 56 μm long by 26 to 39 μm wide (average dimensions 46 x 32 μm).

Distribution: This taxon occurs sporadically making it difficult to evaluate its temporal and spatial distribution. Due to its large size, it can contribute significantly to ciliate biomass some occasions.

References:

Corliss, J.O. 1979. *The Ciliated Protozoa: Characterization, Classification and Guide to the Literature.* 2nd Ed. Pergamon Press. London (p. 215; Plate XXII, Figs. 29–31).

Curds, C.R. 1982. *British and Other Freshwater Ciliated Protozoa.* Part I. Cambridge Univ. Press, Cambridge, England (p. 103; Fig. 57).

Small, E.B. and D.H. Lynn. 1985. Phylum Ciliophora. In *Illustrated Guide to the Protozoa*, J.J. Lee, S.H. Hutner, and E.C. Bovee (eds.). Society of Protozoology, Lawrence, KS. (p. 465; Fig. 15).

Comments: This taxon appears to be more abundant in Lake Ontario (Taylor and Heynen, 1987) compared with the three upper Great Lakes sampled here. Its occurrence might be an indicator of a more eutrophic condition. A second smaller taxon of the genus *Coleps* (24 x 15 μm) also occurs in the upper Great Lakes.

Phylum: Ciliophora
Order: Sessilida

Ciliates belonging to this order are generally sedentary, with cells often attached to substrata via a stalk. These organisms are well represented in both marine and freshwater, where they are suspension-feeders on bacteria and small plankton. Some appear to remain suspended and can occur in the pelagica through attachment to other planktonic organisms. This group is most commonly considered a suborder in the order Peritrichida (see Corliss, 1979), which presents 12 families within the suborder. The taxonomic presentation of Curds et al. (1983) treats the Sessilids at the level of suborder, but does not include a description of families. The suborder was raised to the ordinal level by Small and Lynn (1985), wherein they also observe 12 families, only one of which (Zoothamniidae) differs from those presented by Corliss. Two of the 12 families described by these investigators are pertinent to our work here: Vaginacolidae and Vorticellidae. Both consist of species present in the plankton of the upper Great Lakes.

The cell body of sessilids is generally goblet- or bell-shaped to cylindrical; some groups are entirely loricate. A conspicuous array of buccal cilia winds about the apical face of the cells, and somatic ciliature is usually reduced to a subequatorial fringe. Most individuals are sedentary or sessile with very little power of secondary locomotion. Cells can be solitary or exist in colonies, usually on a variety of substrata (epizooic to epiphytic). A contractile vacuole leads into a ciliated oral cavity, at the base of which is the cytosome.

Members of this order are present in most samples collected from the Great Lakes (Taylor and Heynen, 1987; Carrick and Fahnenstiel, 1990). Taxonomic profiles of three taxa are presented herein. Only one other form that has been tentatively identified as *Zoothamnium,* was observed during this study. The difficulty in identifying members of this order from preserved material (due to contraction of the specimens) leaves open the possibility that other taxa may exist in the upper Great Lakes that we have yet to identify.

Phylum: Ciliophora
Order: Sessilida
Taxon: *Vaginacola* sp.

Description: Cells occur in a cup-shaped lorica aborally attached to a host substratum (without a stalk). Cells are solitary or in groups of two within a common lorica (Plate VI, Figure 33). Cell body is bell-shaped, but appears oblong following preservation. A contractile vacuole leads into a ciliated oral cavity, at the base of which is the cytosome. Buccal cilia winds about the apical pole, and the body ciliature is reduced to a subequatorial fringe. The range in diameter size for this taxon is from 16 to 20 µm (average size 18 µm).

Distribution: *Vaginacola* was generally rare in samples, yet some between-lake differences may exist. In Lake Huron, this taxon was present in samples collected during the winter to spring isothermal period (range 20 to 200 cells L^{-1}), when it was not present in Lake Michigan. Following thermal stratification in both lakes, it occurred in or below the metalimnion (20–50 m).

References:

Corliss, J.O. 1979. *The Ciliated Protozoa: Characterization, Classification and Guide to the Literature*. 2nd Ed. Pergamon Press. London (p. 276; Plate XXIX, Figs. 86–93).

Curds, C.R., M.A. Gates, and D. McL. Roberts. 1983. *British and Other Freshwater Ciliated Protozoa*. Part II. Cambridge Univ. Press, Cambridge, England (p. 258; Fig. 158).

Small, E.B. and D.H. Lynn. 1985. Phylum Ciliophora. In *Illustrated Guide to the Protozoa*, J.J. Lee, S.H. Hutner, and E.C. Bovee (eds.). Society of Protozoology, Lawrence, KS. (p. 548; Fig. 12).

Comments: This taxon is found either free floating or attached to large planktonic diatoms.

Phylum: Ciliophora
Order: Sessilida
Taxon: *Vorticella* sp.1

Description: These aloricate cells occur solitarily or gregariously being attached to a host substratum with a contractile stalk (Plate VI, Figure 34). Cell body is ovoid, but appears more spherical following preservation. A contractile vacuole leads into a ciliated oral cavity, at the base of which is the cytosome. Buccal cilia wind about the apical pole, and the body ciliature is reduced to a subequatorial fringe. The size of this taxon is from 10 to 20 µm in diameter (average size 13 µm).

Distribution: This taxon was present in the water column throughout the year (range 20 to 1,000 cells L^{-1}). It reached its peak abundance as the deep chlorophyll layer developed following thermal stratification (June–July).

References:

Corliss, J.O. 1979. *The Ciliated Protozoa: Characterization, Classification and Guide to the Literature.* 2nd Ed. Pergamon Press. London (p. 273; Plate XXIX, Figs. 1–12).

Curds, C.R., M.A. Gates, and D. McL. Roberts. 1983. *British and Other Freshwater Ciliated Protozoa.* Part II. Cambridge Univ. Press, Cambridge, England (p. 260; Fig. 159).

Small, E.B. and D.H. Lynn. 1985. Phylum Ciliophora. In *Illustrated Guide to the Protozoa*, J.J. Lee, S.H. Hutner, and E.C. Bovee (eds.). Society of Protozoology, Lawrence, KS. (p. 465; Fig. 15).

Comments: This taxon is commonly found either free floating in the water column or attached to host cells. During spring isothermy, it is dispersed throughout the water column, but during thermal stratification it tends to be attached to large planktonic diatoms in the deep chlorophyll layer.

Phylum: Ciliophora
Order: Sessilida
Taxon: *Vorticella companula*

Description: These aloricate cells occur solitarily or gregariously being attached to a host substratum with a contractile stalk (Plate VI, Figure 35). Cell body is bell-shaped, but appears spherical following preservation. A contractile vacuole leads into a ciliated oral cavity, at the base of which is the cytosome. Buccal cilia wind about the apical pole, and the body ciliature is reduced. The taxon is from 20 to 33 µm in diameter (average size 25 µm).

Distribution: This taxon only occurred in the surface waters during thermal stratification (range 200 to 2,500 cells L^{-1}). It grew attached to large masses of the filamentous cyanobacterium *Anabaena flos-aquae* (Lyngb.)deBribisson.

References:

Corliss, J.O. 1979. *The Ciliated Protozoa: Characterization, Classification and Guide to the Literature.* 2nd Ed. Pergamon Press. London (p. 273; Plate XXIX, Figs. 1–12).

Curds, C.R., M.A. Gates, and D. McL. Roberts. 1983. *British and Other Freshwater Ciliated Protozoa.* Part II. Cambridge Univ. Press, Cambridge, England (p. 260; Fig. 159).

Small, E.B. and D.H. Lynn. 1985. Phylum Ciliophora. In *Illustrated Guide to the Protozoa*, J.J. Lee, S.H. Hutner, and E.C. Bovee (eds.). Society of Protozoology, Lawrence, KS. (p. 465; Fig. 15).

Comments: Attachment by *Vorticella* to *Anabaena* colonies has been observed elsewhere (Pratt and Rosen, 1983). This symbiosis may function to keep this species suspended in the water column, as well as providing it with a refuge from predation (Carrick et al., 1991). This taxon is distinguished from *Vorticella* sp.1 by its larger size and more distinct bell-shaped cells.

SUMMARY

The planktonic protozoan assemblage in the upper Great Lakes (Huron, Michigan, and Superior) is a diverse and consistent component of the pelagic community in each of these lakes. While we restricted our analysis here to only the most common forms, more than 100 distinct taxa have been recognized overall (Carrick, 1990; G.L. Fahnenstiel, unpubl. data). The 35 taxa presented herein span five orders of the Phylum Sarcomastigophora (flagellated forms) and four orders of the Phylum Ciliophora (ciliated forms). Species of both groups occur throughout the year, with the exception of Lake Superior where we have no information on the Ciliophora. Ameboid protozoa (Phylum Sarcomastigophorea, Subphylum Sarcodina) were observed on certain occasions, although we did not routinely estimate their abundance and biomass. In addition, no representatives of the third Subphylum Opalinata in the Phylum Sarcomastigophorea were observed; this group is entirely parasitic (Lee et al., 1985).

Our data indicate that the Great Lakes protozoa are structurally diverse. The range in size among taxa varies more than two orders of magnitude (range from 2 to 228 µm). This level of variation is truly unique and is comparable with the size range from bacteria to metazoa (Fenchel, 1987). The average size of nano-protozoa (3–4 µm) and micro-protozoa (21 µm) in all three lakes is small due to the prevalence of small chrysomonads, choreotrichs, and oligotrichs. Similarly, the morphology of the Great Lakes protozoa is also quite variable. Species exhibit simple cell geometries, such as spherical or ovoid shape (i.e., Chrysomonadida: *Chromulina*). More complex forms are also common, whereby the cell body is modified with arm-like projections (Dinoflagellida, *Ceratium hirudinella*) or extended oral regions (Haptorida: *Mesodinium* sp., *Monodinium* sp.). In some cases, this range in morphology can be observed within a single order.

Protozoa are abundant in all three of the upper Great Lakes (from 10^2 to 10^4 cells mL^{-1}), and the composition among lakes is similar. Intensive surveys in Lakes Huron and Michigan (Carrick and Fahnenstiel, 1989; Carrick and Fahnenstiel, 1990) indicate the quantitative importance of protozoa. Based upon annual averages, nearly 50% of phytoplankton biomass is accounted for by phototrophic protozoa, while heterotrophic protozoa constitute 80% of macrozooplankton biomass. The protozoa encountered in this study were distributed heterogeneously with depth, such that a distinct subsurface (20–40 m) protozoan assemblage developed in all three lakes once the water column stratified. The community is composed of cryptomonads (e.g., *Cryptomonas* species and *Rhodomonas minuta*), dinoflagellates (*Gymnodinium helveticum*), choreotrichous ciliates (particularly tintinniids *Codonella cratera* and *Tintinnidium* sp.1), and oligotrichous ciliates (*Strombidium* species).

Protozoa occupy a variety of trophic niches in the upper Great Lakes, based upon our initial studies of food web dynamics. For example, numerous species appear to be active bacterivores (*Chromulina* and *Strobilidium* sp.1), while some phototrophs such as *Rhodomonas minuta* (Fahnenstiel et al., 1991), *Chrysochromulina parva* (H.J. Carrick, unpubl. data), and *Gymnodinium helveticum* (Frey and Stoermer, 1980; Carrick et al., 1992) have been observed to ingest prey. On the other hand, several species contain intracellular chlorophyll-bodies (*Pelagohalteria* and *Pelagostrombidium*). This phenomenon has been observed elsewhere (Pace, 1982; Taylor and Heynen, 1987) and some experimental evidence exists to show these or other similar species are photosynthetically capable (Stoecker et al., 1989). While we have not determined whether the chlorophyll-bearing ciliates in the Great Lakes are photosynthetic, this is most likely the case. This diversity of trophic relationships among the protozoa indicate that the trophic couplings between phytoplankton-macrozooplankton-fish is not necessarily the major carbon pathway in the upper Great Lakes (see Scavia, 1988).

Regardless, the quantitative and qualitative importance of planktonic protozoa in the Great Lakes has been demonstrated (Pick and Caron, 1987; Taylor and Heynen, 1987; Carrick and Fahnenstiel, 1989, 1990). This guide presents holistic, ecological information on the abundant taxa occurring in the upper Great Lakes, and adds to this contention. Our data was derived using more conventional microscopic techniques routinely employed in ecological studies (epifluorescence and light microscopy). Thus, our emphasis lies in the identification and description of major morphotypes as defined by those characteristics visible with these techniques. We hope the guide will be of use to those interested in the planktonic protozoa from a variety of systems, including the Great Lakes.

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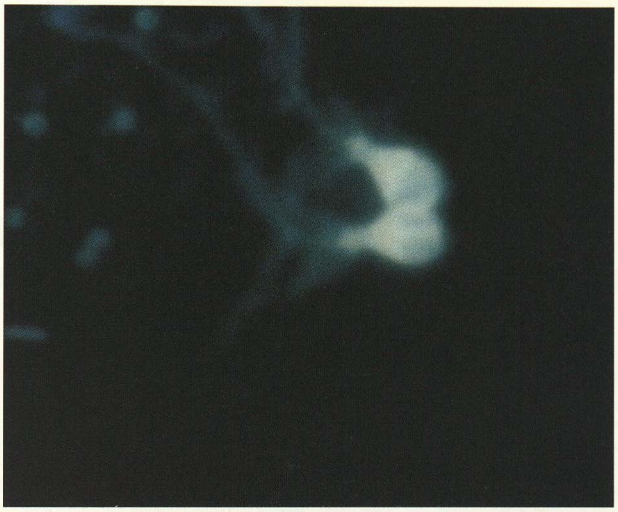

Figure 1. *Desmarella* sp. (epifluorescent, ca. 1,500x).

Figure 2. *Chromulina* sp. (epifluorescent, ca. 2,000x).

Figure 3. *Chromulina* minima (epifluorescent, ca. 2,000x).

Figure 4. *Ochromonas nana* (epifluorescent, ca. 4,000x).

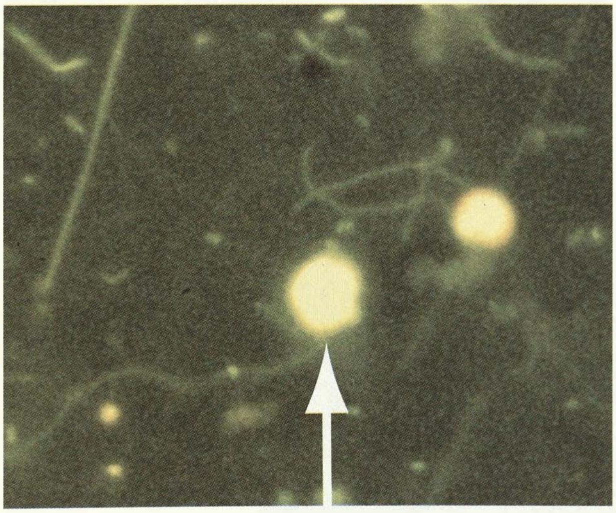

Figure 5. *Ochromonas ovalis* (epifluorescent, ca. 1,400x).

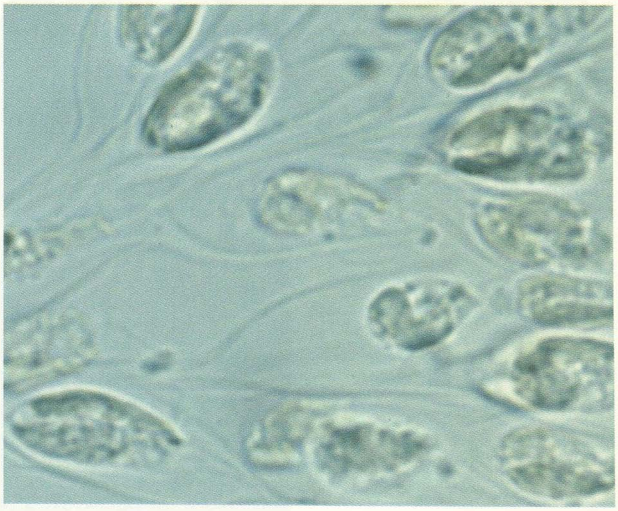

Figure 6. *Dinobryon divergens* (brightfield, ca. 1600x).

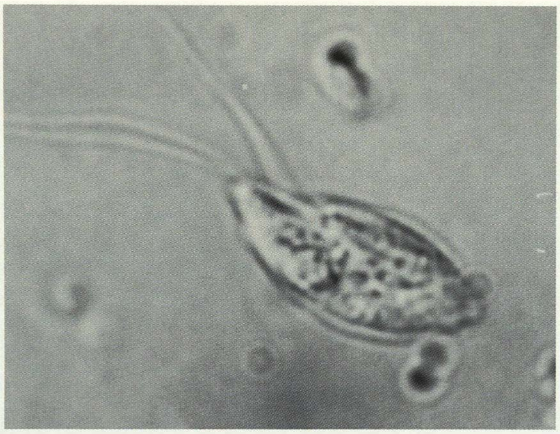

Figure 7. *Cryptaulax* sp.1 (brightfield, ca. 3600x).

Figure 8. *Cryptomonas erosa* (brightfield, ca. 1000x).

Figure 9. *Cryptomonas erosa var. reflexa* (brightfield, ca. 700x).

Figure 10. *Cryptomonas ovata* (brightfield, ca. 2500x).

Figure 11. *Katablepharis ovalis* (brightfield ca. 1900x).

Figure 12. *Rhodomonas lens* (brightfield, ca. 2000x)

Figure 13. *Rhodomonas minuta* (brightfield, ca 3000x)

Figure 14. *Ceratium hirudinella* (brightfield, ca. 400x).

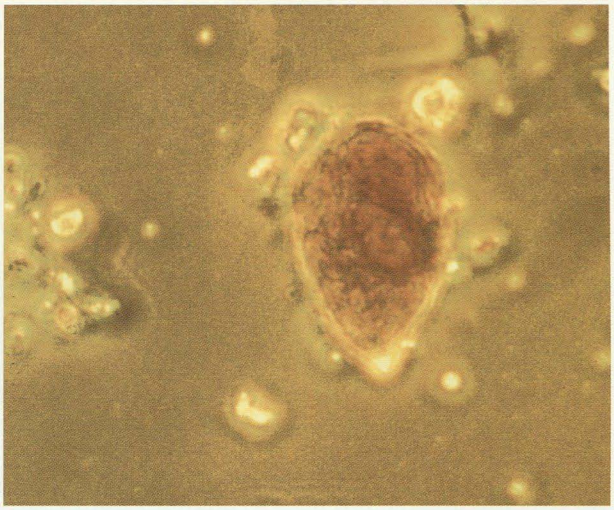

Figure 15. *Gymnodinium helveticum* (brightfield. ca. 800x).

Figure 16. *Gymnodinium varians* (epifluorescent, ca. 1600x).

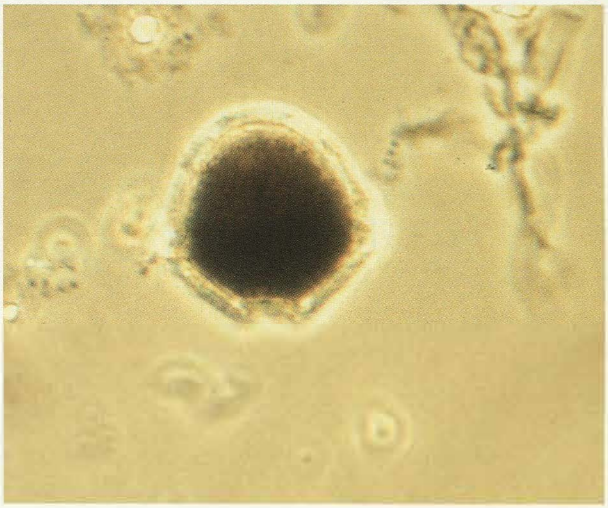

Figure 17. *Peridinium inconspicuum* (brightfield, ca. 1200x).

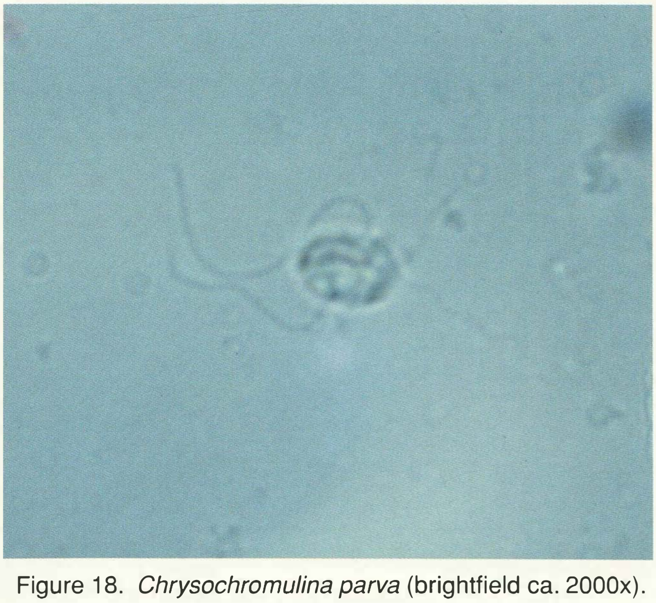

Figure 18. *Chrysochromulina parva* (brightfield ca. 2000x).

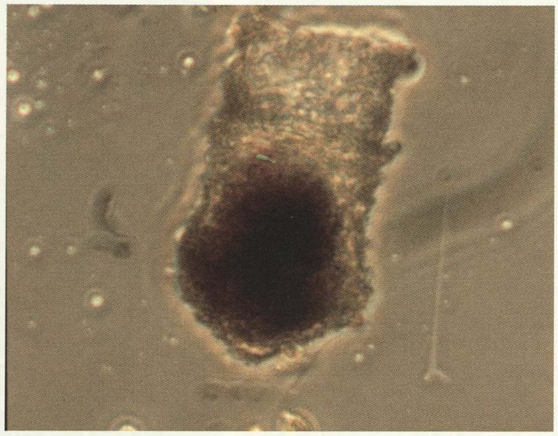

Figure 19. *Codonella cratera* (brightfield, ca. 400x).

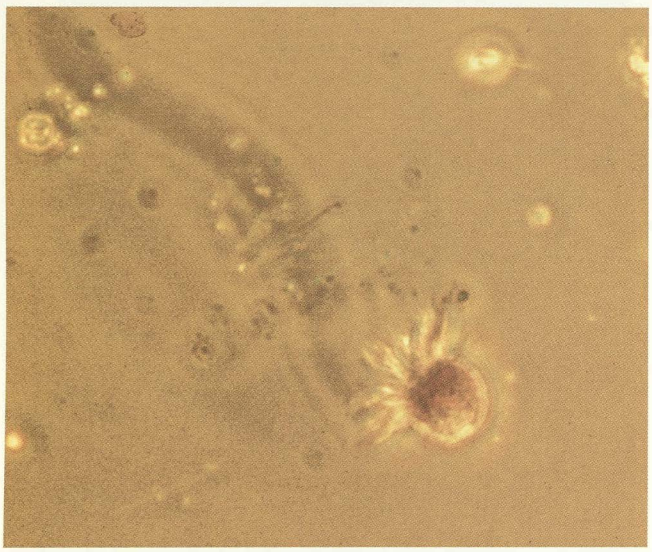

Figure 20. *Strobilidium* sp.1 (brightfield, ca. 800x).

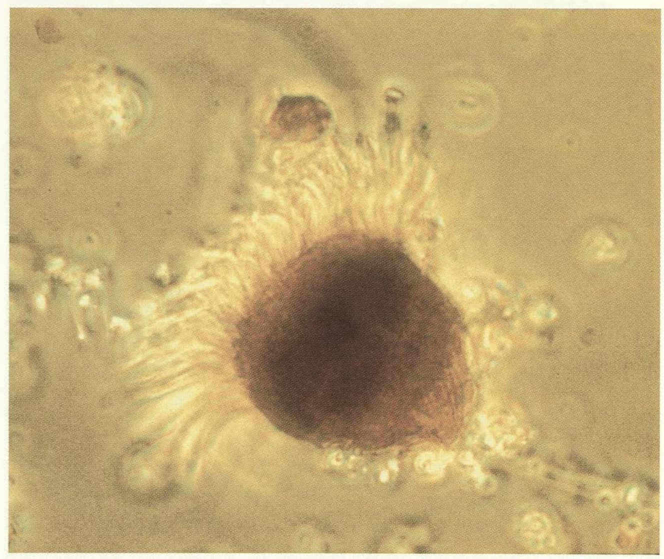

Figure 21. *Strobilidium velox* (brightfield, ca. 1000x).

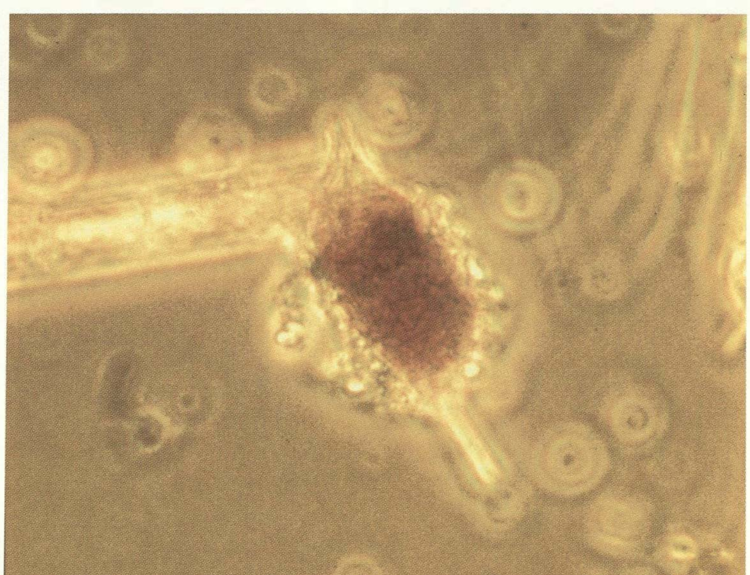

Figure 22. *Tintinnidium* sp.1 (brightfield, ca. 1000x).

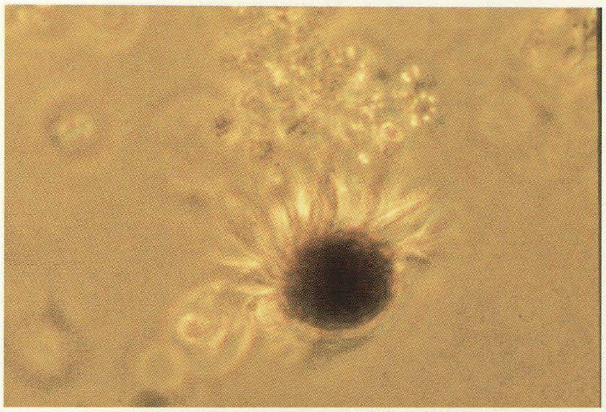

Figure 23. *Pelagohalteria* sp.1 (brightfield, ca. 800x).

Figure 24. *Strombidium* sp.1 (brightfield, ca. 1000x).

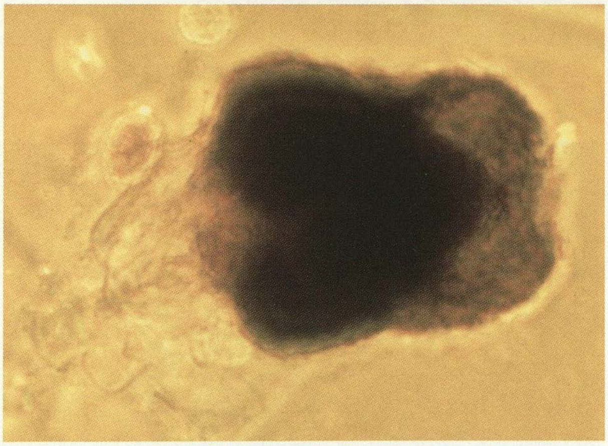

Figure 25. *Pelagostrombidium* sp.1 (brightfield, ca. 1000x).

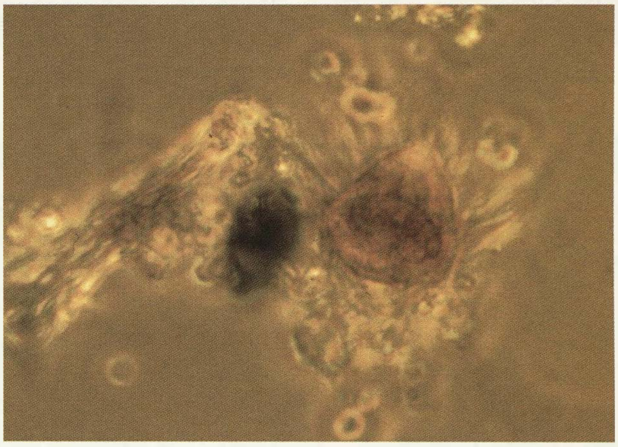

Figure 26. *Askenasia* sp.2 (brightfield, ca. 400x).

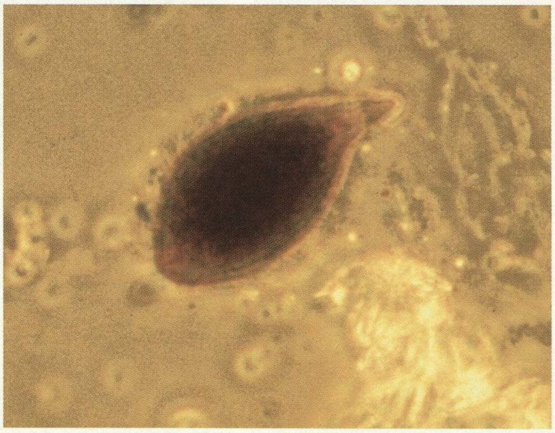

Figure 27. *Lagynophyra* sp.1 (brightfield, ca.1000x).

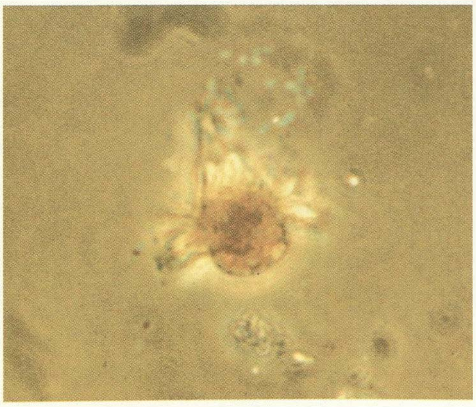

Figure 28. *Mesodinium* sp. (brightfield, ca. 400x).

Figure 29. *Monodinium* sp.2 (brightfield, ca.1000x).

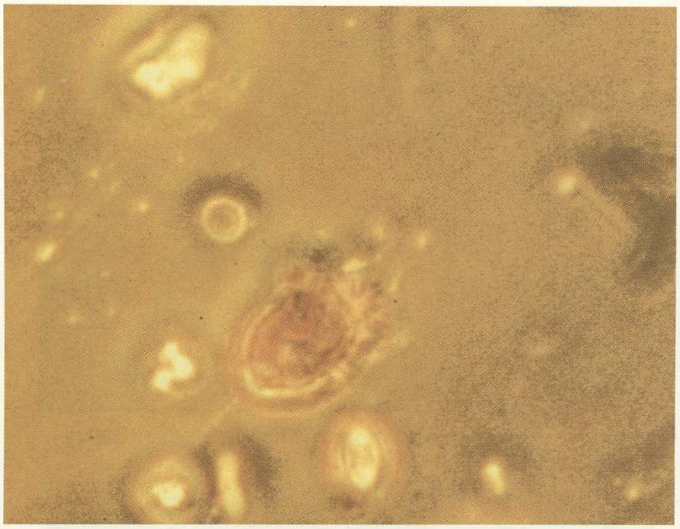

Figure 30. *Pseudobalanion* sp. (brightfield, ca. 800x).

Figure 31. *Urotricha* sp.1 (brightfield, ca. 700x).

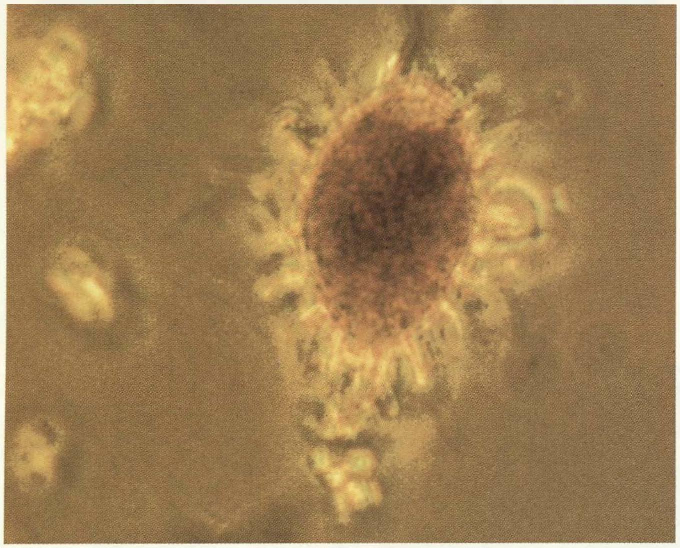

Figure 32. *Coleps* sp.2 (brightfield, ca. 800x).

Figure 33. *Vaginacola* sp. (brightfield, ca. 1000x).

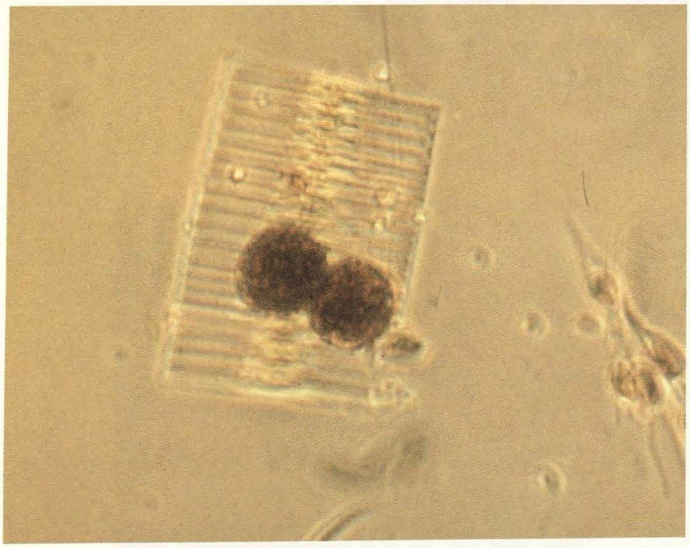

Figure 34. *Vorticella* sp.1 (brightfield, ca. 1000x).

Figure 35. *Vorticella campanula* (brightfield, ca. 600x).