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The scaled chrysophyte flora of Cape Cod, Massachusetts, USA, with special emphasis on lake water chemistry

by

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With 9 figures and 2 tables

Abstract: A total of 43 scaled chrysophyte taxa were observed in plankton collections made from 60 lakes and ponds on the peninsula known as Cape Cod, a peninsula extending into the Atlantic Ocean along the northeastern coast of the United States between 41°30' and 42°00' North latitude. The water-bodies, primarily seepage lakes of glacial origin, are characterized as largely acidic, poorly buffered and oligotrophic in nature, with relatively high concentrations of sodium, chloride and magnesium. The number of taxa found per lake ranged from 0 to 15 with a mean of 7. The most important species included *Mallomonas caudata, Mallomonas acaroides* var. *muskokana, Mallomonas hamata* and *Mallomonas duerrschmidtiae*, while taxa of the genus *Synura* were common or abundant in only a few of the waterbodies. Despite the small geographic area represented by Cape Cod, there were clear differences in the distributions of species along a transect from the mainland out onto the peninsula. In general, one group of taxa were found in significantly more of the lakes and ponds near the mainland and declined in importance and abundance with distance out onto the peninsula. Another group of organisms clearly became more abundant with distance out onto the Cape. The differences in the geographic distributions of the taxa are discussed in relation to differences in water chemistry.

Key words: Scaled chrysophytes, Cape Cod, synurophytes, distribution, ecology, acid lakes.

Introduction

Scale-bearing Chrysophyceae and Synurophyceae, referred to collectively as scaled chrysophytes, are freshwater planktonic flagellates composed of overlapping siliceous scales with species-specific designs. Many species of scaled chrysophytes repeatedly have been found to be restricted along various environmental gradients and, as such, can serve as excellent bioindicators (Kristiansen 1986, Siver 1995). Because many species of scaled chrysophytes are excellent bioindicators and since their species-specific scales become archived in lake sediments, they have been utilized successfully in reconstructing historical lakewater conditions (Smol 1995). Scaled chrysophyte remains have been used to infer pH (e.g. Charles & Smol 1988, Siver & Hamer 1989, Cumming et al. 1992a, Siver et al. 1999), specific conductance (Siver 1993), and trophic-related characteristics (Siver & Marsicano 1996), and Siver et al. (1999) recently used them to study the effects of land use change on lake water chemistry over the last century.

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Cape Cod is a 105 km-long peninsula that protrudes out into the Atlantic Ocean along the southeastern portion of the State of Massachusetts, USA, between 41°30' and 42°00' North latitude. The peninsula, physically separated from the mainland by a man-made canal known as the Cape Cod Canal, was formed during the Wisconsin glaciation period between 10,000 and 15,000 years ago (Strahler 1966). Cape Cod is composed primarily of glacial moraine and glacial outwash deposits, and post-glacial sand dune accumulations (Oldale & Barlow 1986). The thick layer of glacial deposits make the Cape Cod peninsula quite different from any other geologic region in Massachusetts (Mattson et al. 1992) and in nearby Connecticut (Canavan & Siver 1994). The width of the peninsula ranges from 32 km near the canal to only 1.6 km near the outer tip.

There are over 343 ponds and lakes on Cape Cod ranging in size from 4 to 301 hectares. Except for a few ponds situated within the post-glacial sand dune deposits, the majority of the waterbodies are believed to be true glacial kettle holes. Most of the ponds and lakes are seepage lakes that are connected to the groundwater system and lack an inlet and an outlet. The waterbodies can be characterized as acidic, low in alkalinity, and oligotrophic (Mattson et al. 1992, Ahrens & Siver 2000). In practically all of the lakes sodium and chloride are the dominant cation and anion species, respectively, and calcium concentrations are exceptionally low (Ahrens & Siver 2000). Except for the shallow and highly humic ponds situated on the sand accumulations on the outer Cape, the waterbodies are primarily clear water with good light penetration. In a recent survey of 60 of the waterbodies Ahrens & Siver (2000) noted that the lakes were situated along specific chemical gradients. In general, along a distance axis from the Cape Cod Canal out to the outer portion of the Cape lakes decrease in pH, increase in sodium, chloride and magnesium concentrations, and become slightly more oligotrophic. Based on a principle components analysis (PCA) Ahrens & Siver (2000) identified two sets of relatively uncorrelated chemical variables. The lakes were primarily separated along an axis correlated with sodium, chloride, magnesium and specific conductance, and secondarily along an axis related to pH, alkalinity and calcium.

The percentage of acidic lakes with an alkalinity below 0 μeq/l on Cape Cod was found to be greater (Mattson et al. 1992, Ahrens & Siver 2000) than any other region examined in the northeastern United States (Brakke et al. 1988). It is not clear if the high number of very acidic lakes on Cape Cod is related to acidic deposition over the past century, or if the waterbodies are naturally acidic. Based on a paleolimnological study Winkler (1988) concluded that at least some of the ponds on the outer Cape were natually acidic and have been since their formation. Because of the large percentage of poorly buffered lakes and ponds additional paleolimnological studies could provide valuable information concerning historical acidification of the waterbodies.

There were three objectives of the study: firstly, to characterize the scaled chrysophyte flora in the ponds and lakes of Cape Cod in order to provide a sound database for future paleolimnological investigations; secondly, to determine if there were differences in the flora between waterbodies situated along a distance gradient extending out onto the peninsula that may be related to differences in water chemistry; and finally to compare the flora to other temperate regions in North America.

Study area

In a recent study detailing the chemistry of 60 lakes on Cape Cod, Ahrens & Siver (2000) divided these lakes and ponds into four regions based on geology (Strahler 1966) and geographic location relative to the Cape Cod Canal (Fig. 1): 1) The "Bicep" is the region closest to the Cape Cod Canal and consists of Mashpee Pitted outwash plain deposits and portions of

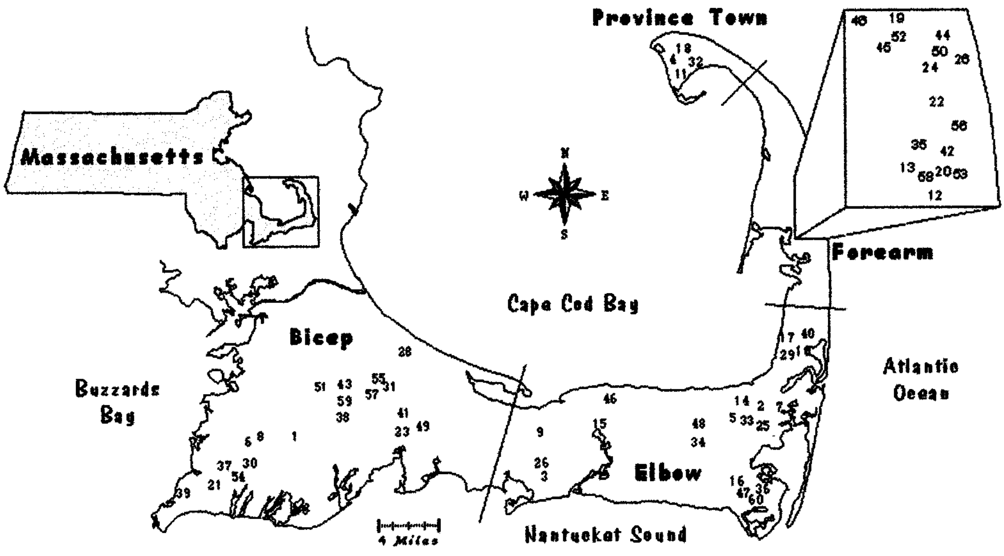


Fig. 1. Map of the Cape Cod peninsula located off the coast of Massachusetts showing the locations of the 60 study lakes. Note the four geographic zones, the Bicep, the Elbow, the Forearm and Provincetown. The numbers refer to those listed in Table 1. See text for details.

the Sandwich moraine; 2) the "Elbow" is the next region consisting of Eastham and Harwich outwash plain deposits; 3) the "Forearm" is located on the portion of the penisula that bends towards the north and is composed of Wellfleet outwash plain deposits and; 4) the region identified as "Provincetown" is located on the outer most tip of the peninsula and consists of post-glacial dune deposits (Oldale & Barlow 1986).

Except for the four lakes in the Provincetown region, all of the waterbodies are believed to be true glacial kettle holes, and except for five additional ponds (Ahrens & Siver 2000) the remaining 51 are believed to be true seepage lakes. The ponds ranged in surface area from 3.6 ha to 301 ha and in maximum depth from 1 m to 26 m.

Methods

Plankton samples were collected from 60 lakes and ponds on Cape Cod, including 19, 21, 16 and 4 from the Bicep, Elbow, Forearm and Provincetown regions, respectively (Table 1; Fig. 1). The numbers on Fig. 1 correspond to those listed for each lake or pond in Table 1. Waterbodies in the Forearm region were sampled in October, 1996, and all others in June, 1997. All lakes were sampled a second time in July, 1997 for a total of 120 collections. Both water samples and plankton-net samples (10 µm mesh) were used to analyse the scaled chrysophyte flora. Approximately 1 ml of the plankton-net concentrate was air dried soon after collection onto a piece of heavy duty aluminum foil. The water samples were fixed with Lugol's, concentrated by centrifugation and an aliquot was air dried onto a piece of aluminum foil.

Each piece of aluminum foil was trimmed, mounted onto an aluminum stub with Apiezon wax, coated with a gold and palladium mixture with a Polaron sputter coater, and observed with either a Leo 982 or a Leo 435V scanning electron microscope (SEM). All identifications were made with SEM and the relative abundances qualitatively estimated according to the

Table 1. The 60 lakes and ponds located on Cape Cod that were surveyed for scaled chrysophytes. The lakes are grouped according to region (see text) and the Lake # refers to those listed on Fig. 1. Data for pH and sodium and chloride concentrations are taken from Ahrens & Siver (2000).

Region	Lake	Lake #	pH	[Na^+] (μeq/l)	[Cl^-] (μeq/l)
Bicep	Ashumet	1	7.5	382	369
	Crooked	6	6.9	409	369
	Deep	8	6.9	329	327
	Grews	21	6.8	249	255
	Hamblin	23	7.1	355	341
	Hoxie	28	6.5	487	557
	Jenkins	30	7	381	348
	Lawrence	31	6.1	272	295
	Mares	37	6.6	303	309
	Mashpee	38	7.3	340	337
	Miles	39	5.9	300	336
	Mystic	41	7.1	396	414
	Peters	43	7.1	308	309
	Shubael	49	6.9	487	529
	Snake	51	6.5	282	253
	Spectacle-F	54	6.6	359	337
	Spectacle-S	55	6.4	290	313
	Triangle	57	6.5	307	309
	Wakeby	59	7.4	352	341
Elbow	Baker	2	6.6	479	539
	Big Sandy	3	5.6	559	608
	Cliff	5	7	401	433
	Crystal-O	7	6.3	549	673
	Dennis	9	4.9	372	415
	Depot	10	6.6	611	742
	Flax-B	14	6.6	459	488
	Flax-D	15	4.4	344	369
	Goose	16	6.3	428	507
	Great-E	17	7.1	700	834
	Higgins-B	25	6.4	438	488
	Horse-Y	26	4.7	383	419
	Jemima	29	5.6	451	553
	Little Cliff	33	6	386	415
	Long-B	34	6.5	453	489
	Lovers	36	8	923	820
	Minister	40	6.3	1,552	1,368
	Scargo	46	7.2	588	654
	Schoolhouse	47	7.1	432	493
	Sheep	48	6.6	354	401
	White	60	7.3	1,350	1,198
Forearm	Duck-W	12	4.8	544	725
	Dyer	13	4.7	439	553
	Great-T	19	5.9	636	871
	Great-W	20	4.8	586	788
	Gull	22	6.8	718	919
	Herring-W	24	6.6	674	947
	Horseleech	27	6.3	956	1,210
	Long-W	35	4.7	464	609

Table 1, continued.

Region	Lake	Lake #	pH	$[Na^+]$ (μeq/l)	$[Cl^-]$ (μeq/l)
Forearm	Northeast	42	5.1	542	719
	Round	44	5.2	718	940
	Ryder	45	4.7	749	871
	Slough	50	5.1	672	873
	Snow	52	5.6	469	648
	Southeast	53	5.1	497	733
	Spectacle-W	56	4.9	807	996
	Turtle	58	4.8	536	747
Provincetown	Clapps	4	5.2	584	768
	Duck-P	11	5.6	645	847
	Great-P	18	5.9	485	640
	Little Bennett	32	4.8	653	892

following system. Taxa that were among the most dominant species of algae in the sample were scored as "abundant". Taxa that were sub-abundant, but still important components of the flora were listed as "common". Taxa that were rare, but represented by whole cells were listed as "rare", and ones where only a few isolated scales were observed as "very rare". Factors of 4, 3, 2 and 1 were assigned to relative abundances of abundant, common, rare and very rare, respectively, and used to weight the occurrence of an organism in a collection in order to determine its importance in a given geographic area.

Water samples also were taken over the deep basin of each lake at 1 m and used to measure 13 chemical parameters, including pH, alkalinity, specific conductance, and concentrations of sodium and chloride (Ahrens & Siver 2000). Details of analytical methods and results for all lakes and ponds are presented in Ahrens & Siver (2000). Briefly, pH was measured with a Fisher Accumet model 640A pH meter. Conductivity was measured with a YSI model 33 SCT meter and standardized to specific conductance at 25 °C. Alkalinity was estimated using the Gran titration method (Wetzel & Likens 1991). Sodium concentrations were determined with a Perkin Elmer 2380 atomic absorption spectrophotometer, and chloride concentrations with the argentometric method (Canavan & Siver 1994).

Results

Water chemistry

Although details of the chemistry of the study lakes is given in Ahrens & Siver (2000) a brief summary is presented here (Table 1). The pH of the study lakes ranged from 4.4 to 8.0 with a mean value of 6.15. Eighty percent of the lakes and ponds had a pH below 7, and the pH generally declined with distance out onto the peninsula from the Canal. The mean pH of lakes in the Bicep, Elbow, Forearm and Provincetown were 6.8, 6.3, 5.3 and 5.4, respectively. The study lakes also were poorly buffered with a mean alkalinity of only 39 μeq/l. Thirty-seven percent had alkalinity values below 0 μeq/l, and 63 % had values below 50 μeq/l. A greater percentage of the study lakes located in the Forearm region had alkalinity values below 0 μeq/l.

The specific conductance of all of the study lakes ranged from 54 μS to 206 μS with a mean of 106 μS. In general, the specific conductance values of the lakes in the Forearm and Provincetown regions were double those of lakes in the Bicep region. Sodium was the dominant cation species in the study lakes with a mean concentration of 520 μeq/l, relative to mean concentrations of only 158 µeq/l, 78 µeq/l and 18 µeq/l for magnesium, calcium and potassium, respectively. Mean concentrations of chloride, sulfate and alkalinity anions were 597 µeq/l, 110 µeq/l and 39 µeq/l, respectively for all lakes. In general, the concentrations of sodium, magnesium, and chloride significantly increased with distance from the Canal. In contrast, concentrations of calcium tended to decrease with distance out onto the peninsula, and concentrations of sulfate and potassium were similar across all regions except Provincetown (Ahrens & Siver 2000).

The mean Secchi disk depth for study lakes in the Bicep, Elbow and Forearm were 4.5 m, 4.5 m and 5.0 m, respectively. In contrast, the mean Secchi disk depth for Provincetown lakes was only 0.5 m due to the high humic content. Similarly, total phosphorus concentrations for lakes in the Bicep, Elbow and Forearm were 12 µg/l, 12 µg/l and 10 µg/l, respectively, much lower than the 52 µg/l value for Provincetown lakes. In general, the majority of lakes in the Bicep, Elbow and Forearm regions were oligotrophic or early mesotrophic in nature, whereas those in Provincetown were eutrophic. Mean total nitrogen concentrations of 250 µg/l, 246 µg/l, and 173 µg/l were reported for lakes in the Bicep, Elbow and Forearm, respectively. As a result, except for the Provincetown lakes, there was not a significant change in the trophic status of the study lakes along a distance gradient out onto the peninsula as there was for pH, alkalinity and ionic species.

General characteristics of the scaled chrysophyte flora

The relative abundances of the scaled chrysophytes in the study lakes, as well as for the respective regions, are listed in Table 2, and images of most taxa are found in Figs. 2–6. A total of 43 taxa were found in the study lakes and the number of species per lake ranged from 0 to 15 (Fig. 7). No taxa were reported from five of the lakes, although 22 of the waterbodies harbored eight or more species. The mean number of taxa found per study lake for the Bicep, Elbow, Forearm and Provincetown regions were 6, 6, 9 and 6, respectively.

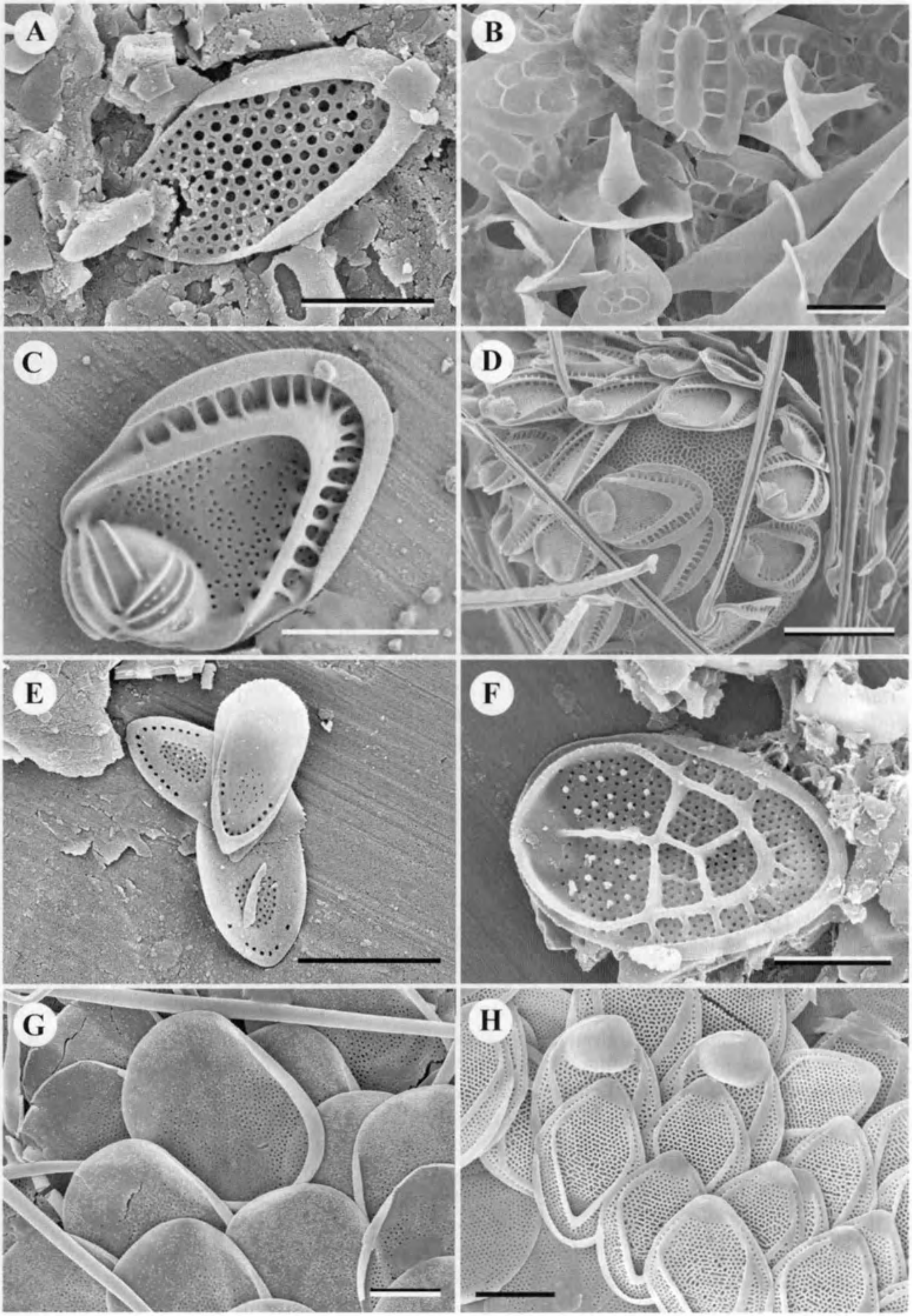
Fifteen of the taxa were found in over 20 % of the study lakes (Table 2; Fig. 8), while fourteen were found in only one or two sites. *Mallomonas caudata* (Fig. 2G), encountered more than any other species, was found in 60 % of the lakes, and three other species, *Mallomonas hamata* (Fig. 3G), *Mallomonas acaroides* var. *muskokana* (Fig. 2C–D) and *Mallomonas duerrschmidtiae* (Fig. 3D), were reported from 43 % or more of the sites. *Synura petersenii* (Fig. 6B) and *Spiniferomonas trioralis* (Fig. 5H) were observed in slightly over one-third of the lakes, and the remainder of the taxa listed in Fig. 8 were found in approximately one-fourth of the localities.

If each occurrence of an organism in a given lake is weighted by its relative abundance as described in the methods section, *M. acaroides* var. *muskokana* and *M. duerrschmidtiae* are approximately equal in importance to *Mallomonas caudata*. However, other often encountered taxa, such as *Mallomonas hamata, Synura petersenii* and *Spiniferomonas trioralis*, decline in importance because they rarely were common or abundant. For example, even though *Mallomonas hamata* and *Synura petersenii* were found in 29 and 22 of the study lakes, they were abundant or common only three and two times, respectively. A group of taxa rarely reported from North America, including *Chrysodidymus synuroideus* (Fig. 2A), *Mallomonas canina* (Fig. 2F), *Mallomonas cyathellata* var. *chilensis* (Fig. 3B), *Mallomonas flora* (Fig. 3F), *Mallomonas paludosa* (Fig. 4C), *Mallomonas parvula* (Fig. 4D), *Spiniferomonas takahashii* (Fig. 5G) and *Spiniferomonas cornuta*, were observed in Cape Cod lakes.

Many of the specimens observed in the study lakes, especially those in the Forearm region, appeared to have scales and bristles that were heavily silicified. Many of the specimens of taxa that produce secondary layers on the shield, such as *Mallomonas duerrschmidtiae*

Table 2. The abundances of species of scaled chrysophytes in waterbodies located on Cape Cod. The percentage of each taxon in all waterbodies, as well as for three regions, the Bicep, the Elbow and the Forearm are given. *Spiniferomonas* sp. represents remains of taxa from this genus that could not be identified to the species level. See text for details.

Taxon	% Abundance			
	All lakes	Bicep	Elbow	Forearm
Chrysodidymus synuroideus Prowse	7	0	0	13
Chrysosphaerella longispina Lauterborn	7	21	0	0
Mallomonas acaroides v. *muskokana* Nicholls	45	42	24	88
Mallomonas akrokomos Ruttner in Pascher	25	26	29	19
Mallomonas canina Kristiansen	13	5	5	25
Mallomonas caudata Ivanov	60	63	71	44
Mallomonas corymbosa Asmund & Hilliard	5	11	5	0
Mallomonas crassisquama (Asmund) Fott	12	26	10	0
Mallomonas cyathellata var. *chilensis* Dürrschmidt	2	0	0	6
Mallomonas dickii Nicholls	3	0	5	6
Mallomonas duerrschmidtiae Siver, Hamer & Kling	43	37	29	81
Mallomonas elongata Reverdin	15	16	24	6
Mallomonas flora Harris & Bradley	2	0	0	6
Mallomonas galeiformis Nicholls	2	5	0	0
Mallomonas hamata Asmund	48	42	43	75
Mallomonas hindonii Nicholls	2	0	0	6
Mallomonas lychenensis Conrad	23	26	5	50
Mallomonas multisetigera Dürrschmidt	7	0	5	13
Mallomonas paludosa Fott	7	0	5	13
Mallomonas papillosa Harris & Bradley	2	0	0	6
Mallomonas parvula Dürrschmidt	3	0	10	0
Mallomonas pseudocoronata Prescott	25	37	24	19
Mallomonas pumilio (Harris & Bradley) em. Asmund, Cronberg & Dürrschmidt	2	0	0	6
Mallomonas punctifera Korsh.	10	11	10	13
Mallomonas sp. 1 (see text)	10	0	5	31
Mallomonas striata Asmund	2	0	5	0
Mallomonas tonsurata Teiling em. Krieger	22	11	19	38
Mallomonas torquata f. *simplex* Nicholls	8	5	10	13
Paraphysomonas vestita (Stokes) De Saedeleer	25	26	29	13
Paraphysomonas takahashii Cronberg & Kristiansen	7	11	5	6
Spiniferomonas bilacunosa Takahashi	10	11	10	6
Spiniferomonas cornuta Balonov	2	0	5	0
Spiniferomonas coronacircumspina (Wujek & Kristiansen) Nicholls	22	32	24	6
Spiniferomonas takahashii Nicholls	2	0	5	0
Spiniferomonas trioralis Takahashi	38	53	48	19
Spiniferomonas sp.	12	16	10	13
Synura echinulata Korsh.	28	11	14	56
Synura echinulata f. *leptorrhabda* Asmund	15	0	14	31
Synura petersenii Korsh.	37	26	38	44
Synura petersenii f. *kufferathii* (Korsh.) Petersen & Hansen	2	5	0	0
Synura sphagnicola Korsh.	23	0	19	56
Synura spinosa Korsh.	23	21	29	19
Synura spinosa f. *longispina* Petersen & Hansen	5	0	5	13
Synura uvella Stein em. Korsh.	12	0	19	6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(Fig. 3D), *Mallomonas tonsurata* (Fig. 5A–B), *Mallomonas pseudocoronata* (Fig. 4E) and *Mallomonas punctifera* (Fig. 4G–H), often had exceptionally thick scales and bristles. The large pores commonly found on the shields of *Mallomonas duerrschmidtiae* and *Mallomonas pseudocoronata* were often observed to be almost closed, and therefore quite small in diameter, due to the thick silica deposits. Other odd morphological structures associated with *Mallomonas acaroides* var. *muskokana* and *Mallomonas duerrschmidtiae* were previously reported by Siver (1999).

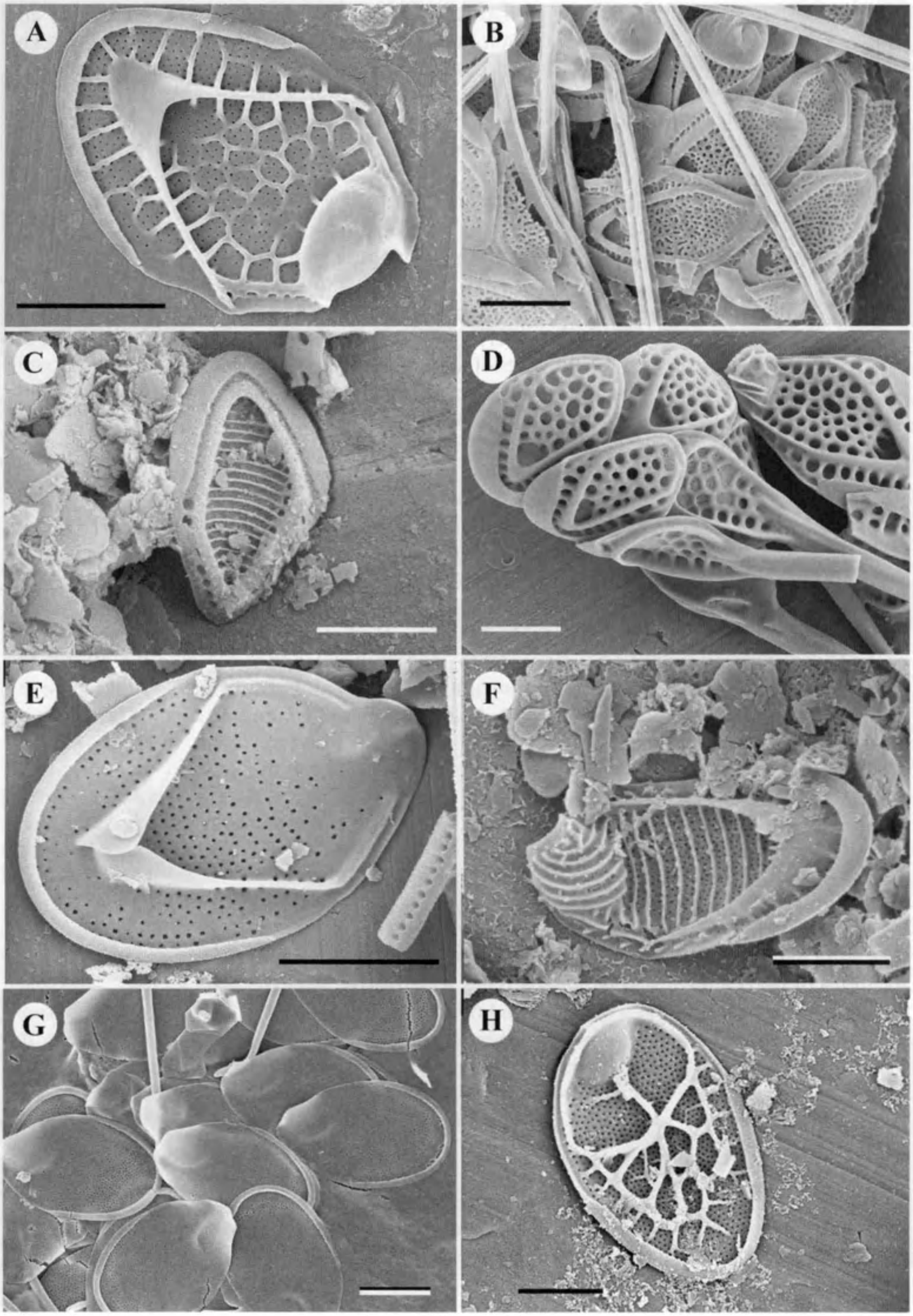
Distribution of selected species between the geographic regions

Many taxa were found to be differentially distributed along a distance gradient from the Canal out onto the peninsula. Because a relatively small number of lakes (4) were included in the Provincetown region, this region will be excluded in this analysis. Three different trends were observed. The first trend was one where taxa decreased in importance with distance out onto the peninsula (Fig. 9A–C); this group included *Chrysosphaerella longispina* (Fig. 2B), *Mallomonas caudata* (Fig. 2G), *Mallomonas corymbosa* (Fig. 2H), *Mallomonas crassisquama* (Fig. 3A), *Mallomonas pseudocoronata* (Fig. 4E), *Paraphysomonas takahashii, Paraphysomonas vestita* (Fig. 5D), *Spiniferomonas coronacircumspina* (Fig. 5E–F) and *Spinferomonas trioralis* (Fig. 5H). *Chrysosphaerella longispina* and *Mallomonas crassisquama* were found in over 20 % of the lakes in the Bicep region, but were absent in all collections made in the waterbodies examined on the outer Cape (Fig. 9). Other species, such as *Mallomonas pseudocoronata, P. takahashii, P. vestita, S. coronacircumspina* and *S. trioralis* were present on the outer Cape, but in significantly fewer of the collections as compared to those observed in the Bicep region (Fig. 9).

A second group of taxa were found in significantly greater occurrence with distance out onto the peninsula (Fig. 9F–H). Even though three of the more common species found in this study, *Mallomonas acaroides* var. *muskokana*, *Mallomonas duerrschmidtiae* and *M. hamata*, were present in 37 % to 42 % of the collections from the Bicep region, they were present in 75 % to 88 % of the collections from the Forearm region (Fig. 9F). *Mallomonas tonsurata* and *S. echinulata,* also members of this second group, were found in over three times as many sites in the Forearm region as compared to the Bicep region (Fig. 9G). Although *Synura sphagnicola* (Fig. 6C) was not found in the Bicep region, it was one of the more common taxa in localities of the outer Cape where it was present in over 50 % of the collections (Fig. 9G). Other taxa, including *Mallomonas canina* (Fig. 2F), *M. paludosa* (Fig. 4C), *M. multisetigera* (Fig. 4B) and *Synura spinosa* f. *longispina*, were also clearly more common in the acidic localities of the outer Cape (Fig. 9H).

The third group of organisms consisted of a few taxa that were found to be slightly more abundant in the central portion of the peninsula, or more-or-less evenly distributed over the distance gradient (Fig. 9D–E). Species in this group included *Mallomonas elongata* (Fig. 3E), *Mallomonas punctifera* (Figs. 4G–H), *Synura spinosa* f. *spinosa* (Figs. 6D–E) and *Synura petersenii* (Fig. 6B). Interestingly, an organism with scales that were similar to those of *M.*

Fig. 2. Scaled chrysophytes from Cape Cod. A. Scale from *Chrysodidymus synuroideus.* Scale bar = 1 µm. B. Group of scales of *Chrysosphaerella longispina.* Scale bar = 2 µm. C–D. Isolated body scale (C) and remains of a whole cell with an immature cyst (D) of *Mallomonas acaroides* v. *muskokana.* Scale bar for C = 2 µm, and 5 µm for D. E. Scales of *Mallomonas akrokomos.* Scale bar = 2 µm. F. Scale of *Mallomonas canina.* Scale bar = 1 µm. G. Group of scales of *Mallomonas caudata.* Scale bar = 2 µm. H. Portion of a cell of *Mallomonas corymbosa.* Scale bar = 2 µm.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punctifera, but lacking the secondary reticulation of ribs (Fig. 4F), was found to be common in localities on the outer Cape. Thus, the distribution of this organism, referred to here as *Mallomonas* sp. 1, had a very different distribution than that of *M. punctifera*. Whereas, *M. punctifera* was equally distributed across the peninsula, *Mallomonas* sp. 1 was found almost exclusively on the outer Cape where it was found in over 30 % of the collections.

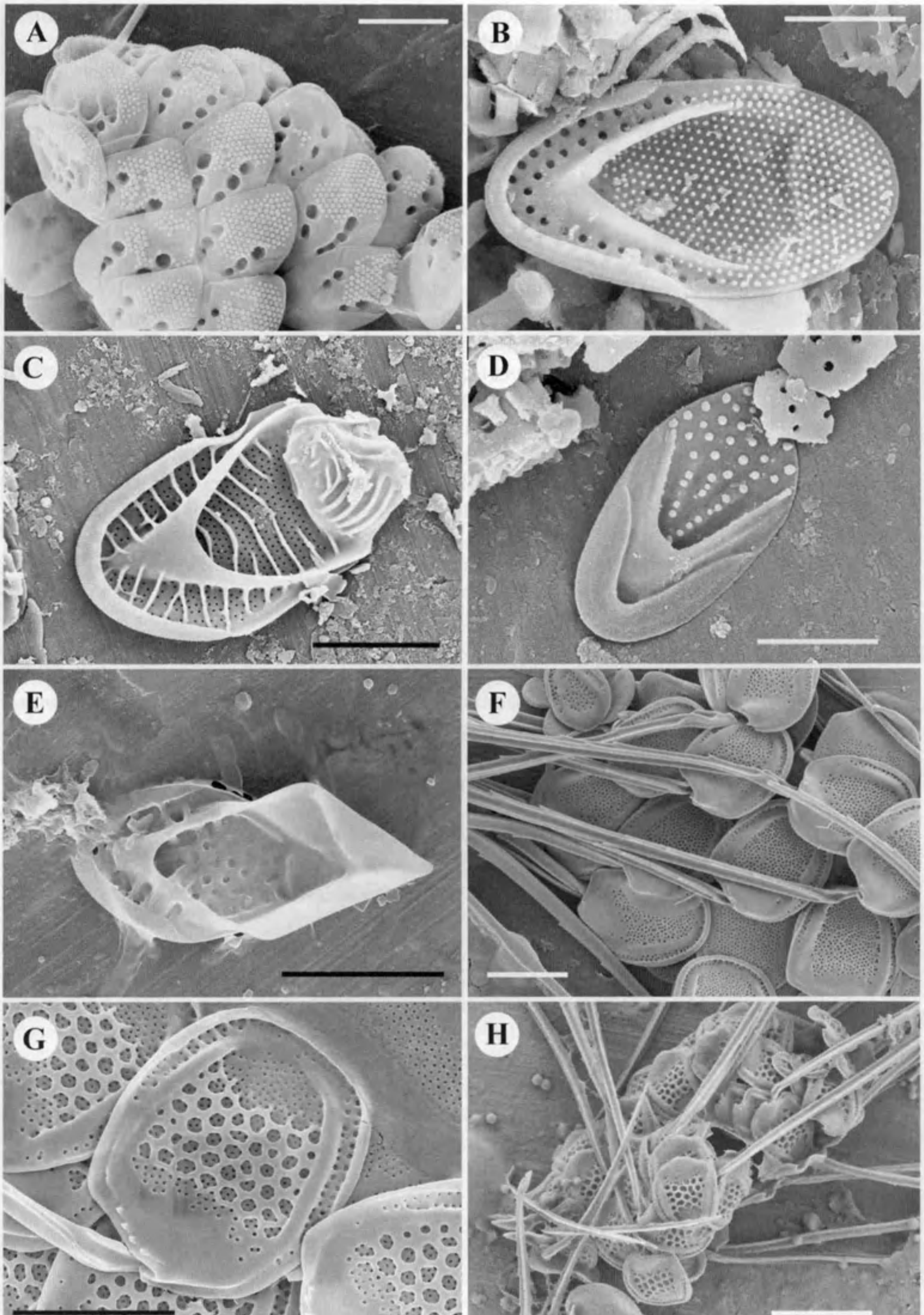
Discussion

It is clear that a rich and diverse flora of scaled chrysophytes exists in the many lakes and ponds on Cape Cod and that the flora has clear affinities with other temperate regions examined in northeastern North America, including Connecticut (e.g. Siver 1987, 1988b, 1991), northern New England (Siver & Lott 2000), the Adirondacks (Smol et al. 1984, Siver 1988a, Cumming et al. 1992b) and adjacent areas of Canada (e.g. Nicholls 1982, Nicholls & Gerrath 1985, Wawrzyniak & Andersen 1985). With a few exceptions, e.g. *Mallomonas cyathellata* var. *chilensis* and *Mallomonas* sp. 1, most of the taxa have been reported previously from temperate regions of North America or Europe. Since collections from the winter months or early spring period were not taken, it is likely that both the number of species encountered and the number of taxa per lake is actually higher, and that the number of lakes with few or no species is probably lower than reported.

One of the most interesting observations made in this study had to do with the distribution of species along a pH gradient. It is well known that many scaled chrysophyte taxa are restricted along a pH gradient (e.g. Siver 1989, 1995). As a result, these organisms are excellent bioindicators of pH and have been utilized successfully in paleolimnological reconstructions (Smol 1995). Indeed, many species commonly reported from habitats with a pH below 6, also were primarily recorded under similar conditions in Cape Cod waterbodies. *Mallomonas canina*, one of the most acidobiontic scaled chrysophytes known (e.g. Eloranta 1985, 1989, Tolonen et al. 1986, Siver 1989), and with a weighted mean pH of 4.9 (Siver 1989), was also found in very acidic localities in this study, and predominantly on the outer Cape. *Mallomonas acaroides* var. *muskokana* has been reported previously to have its maximum development below pH 5, to often disappear above pH 7 (Siver 1991), and with weighted mean pH values of 5.3 (Charles & Smol 1988) and 5.4 (Siver 1989). The distribution of *M. acaroides* var. *muskokana* on Cape Cod, being much more abundant in the acidic localities on the outer part of the peninsula, supports the previous findings for this taxon. Similarly, *Chrysodidymus synuroideus, Mallomonas paludosa, Mallomonas duerrschmidtiae, Synura sphagnicola* and *Synura echinulata* are other acidobiontic or acidophilous taxa that essentially were found under similar conditions on Cape Cod. Other taxa known to be alkaliphilous, such as *Mallomonas corymbosa* and *M. pseudocoronata* (Siver 1991), were more abundant in the less acidic waterbodies of the Bicep region, thus supporting previous ecological records.

Despite the fact that the distributions of many scaled chrysophyte taxa along a pH gradient appeared to correlate well with previous findings, a number of taxa were found in a surprisingly high number of the more acidic sites. The most obvious of these was *Mallomonas ton-*

Fig. 3. Scaled chrysophytes from Cape Cod. A. Body scale of *Mallomonas crassisquama*. Scale bar = 2 µm. B. Portion of a cell of *Mallomonas cyathellata* var. *chilensis*. Scale bar = 2 µm. C. Body scale of *Mallomonas dickii*. Scale bar = 1 µm. D. Group of scales from *Mallomonas duerrschmidtiae*. Scale bar = 2 µm. E. Body scale of *Mallomonas elongata*. Scale bar = 2 µm. F. Scale of *Mallomonas flora*. Scale bar = 1 µm. G. Scales of *Mallomonas hamata*. Scale bar = 2 µm. H. Body scale of *Mallomonas hindonii*. Scale bar = 1 µm.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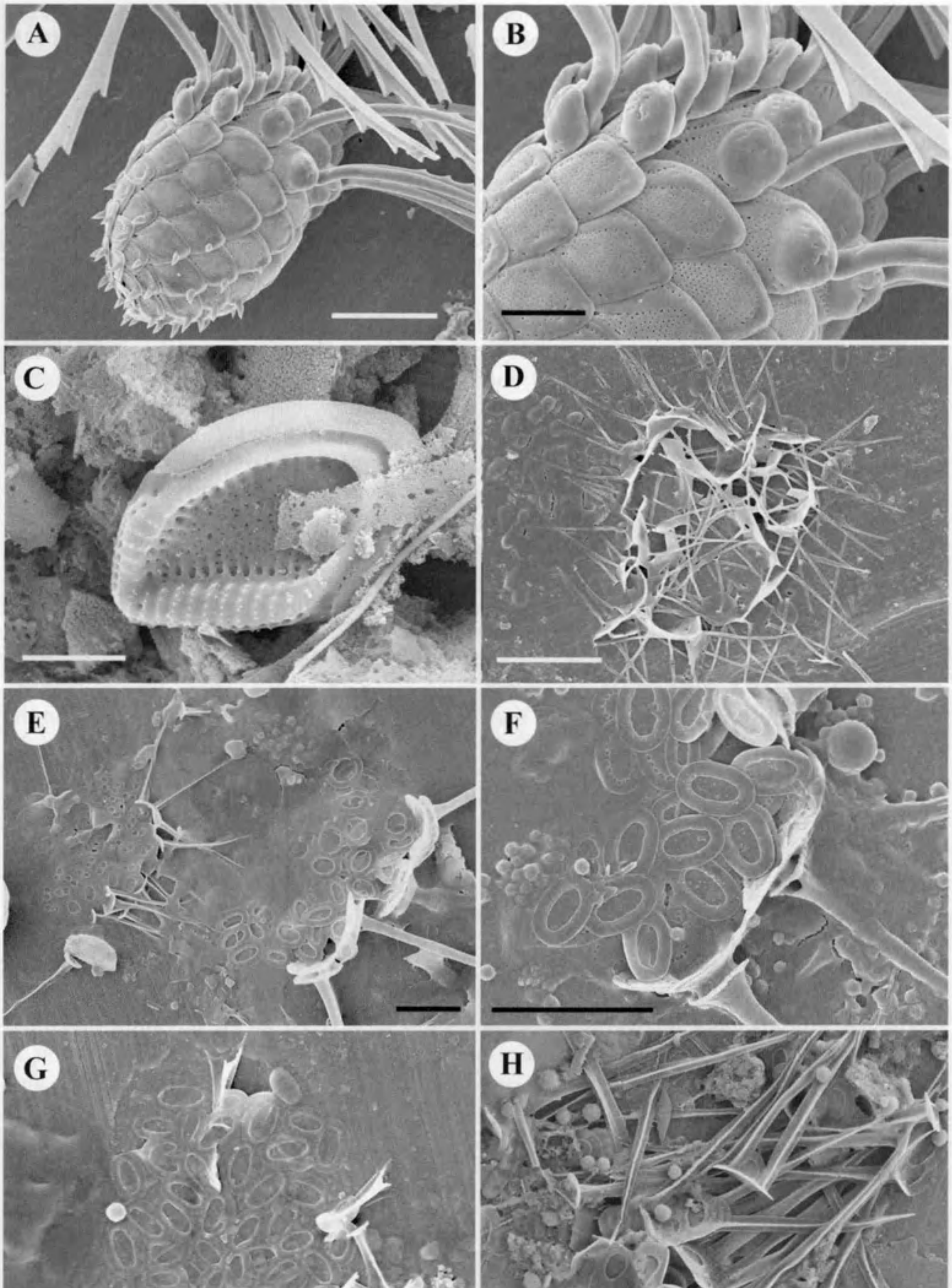
surata, a well documented alkaliphilous or alkalibiontic organism with weighted mean pH values of 7.5 or higher, and rarely found in soft waters below pH 5.5 (Siver 1989, 1991, Gutowski 1997). In this study approximately half of the collections containing *Mallomonas tonsurata* were from localities with pH values below 5.9, and it was found in samples with a pH as low as 4.7. Interestingly, most of the scales of *M. tonsurata* found at pH less than 5 were very heavily silicified. Although *Mallomonas caudata* has been observed over a wide pH range from 4.8 to 9.1 (Siver 1991), it is widely known to be a pH indifferent taxon with a weighted mean pH near 7 (Charles & Smol 1988, Siver 1989, 1991, Gutowski 1997), and to decline significantly in importance as the pH drops below ca. 5.5 to 6. In collections from Cape Cod *M. caudata* often was found in localities with a pH < 6 and it was common in three collections at or below pH 4.7.

The primary chemical difference between these acidic Cape Cod localities and low pH lakes from other regions where alkaliphilous scaled chrysophytes are not commonly found (e.g. the Adirondacks) is in the amount and composition of dissolved ions. For example, acidic, poorly buffered Adirondack lakes and ponds are mostly low in specific conductance with values typically below 30 µS (Siver 1988a). Many of the acidic and poorly buffered Cape Cod lakes, especially those on the outer portions of the Cape, have specific conductance values above 100 µS and have sodium and chloride as the dominant cation and anion species, respectively (Ahrens & Siver 2000). It is possible that the higher sodium ion concentrations, which are an order of magnitude or more higher than the concentrations of hydrogen ions in Cape Cod lakes (Ahrens & Siver 2000), may help to mitigate the effects of high concentrations of hydrogen ions on taxa such as *Mallomonas tonsurata* and *M. caudata*. Clearly, more work is warranted in order to elucidate the physiological basis for why some species are able to thrive in acidic localities on Cape Cod, but not in similarly acidic waterbodies in other regions.

Another interesting observation was the overall lack of importance of organisms in the genus *Synura*. In fact, as a genus, taxa of *Synura* were abundant or common in only ten of the 60 localities. In collections made around the world, *Synura petersenii* is commonly one of the most abundant species of scaled chrysophytes. This certainly is true for most of the regions examined in the northeast part of North America (Siver 1987, 1988a, Nicholls & Gerrath 1985, Cumming et al. 1992b, Siver & Lott 2000). Even though *S. petersenii* was found in 37 % of the collections on the Cape, it was not a dominant taxon at any of the sites and was common at only two localities. In most collections with *S. petersenii* only a few isolated scales were observed.

Like *S. petersenii*, *Mallomonas crassisquama* also has been commonly reported as one of the most important species of scaled chrysophytes (Siver & Skogstad 1988). Siver (1991) reported *M. crassisquama* in over 31 % of collections surveyed from the literature, and it has been reported in over 50 % of waterbodies in some areas (e.g. Hällfors & Hällfors 1988), reinforcing the hypothesis that this organism is one of the more important species of scaled chrysophytes in freshwater habitats. *Mallomonas crassisquama* clearly declined in importance with distance out onto the Cape, and, in fact, was absent from the twenty most eastern localities. The reason for the decline, which occurs within a geographically short distance, is

Fig. 4. Scaled chrysophytes from Cape Cod. A. Cell of *Mallomonas lychenensis*. Scale bar = 2 µm. B. Domed scale of *Mallomonas multisetigera*. Scale bar = 1 µm. C. Domed scale of *Mallomonas paludosa*. Scale bar = 2 µm. D. Isolated scale of *Mallomonas parvula*. Scale bar = 1 µm. E. Body scale of *Mallomonas pseudocoronata*. Scale bar = 5 µm. F. Cell of *Mallomonas* sp. 1. See text for details. Scale bar = 2 µm. G–H. Isolated body scale (G) and remains of a whole cell (H) of *Mallomonas punctifera*. Scale bar = 2 µm for G and 5 µm for H.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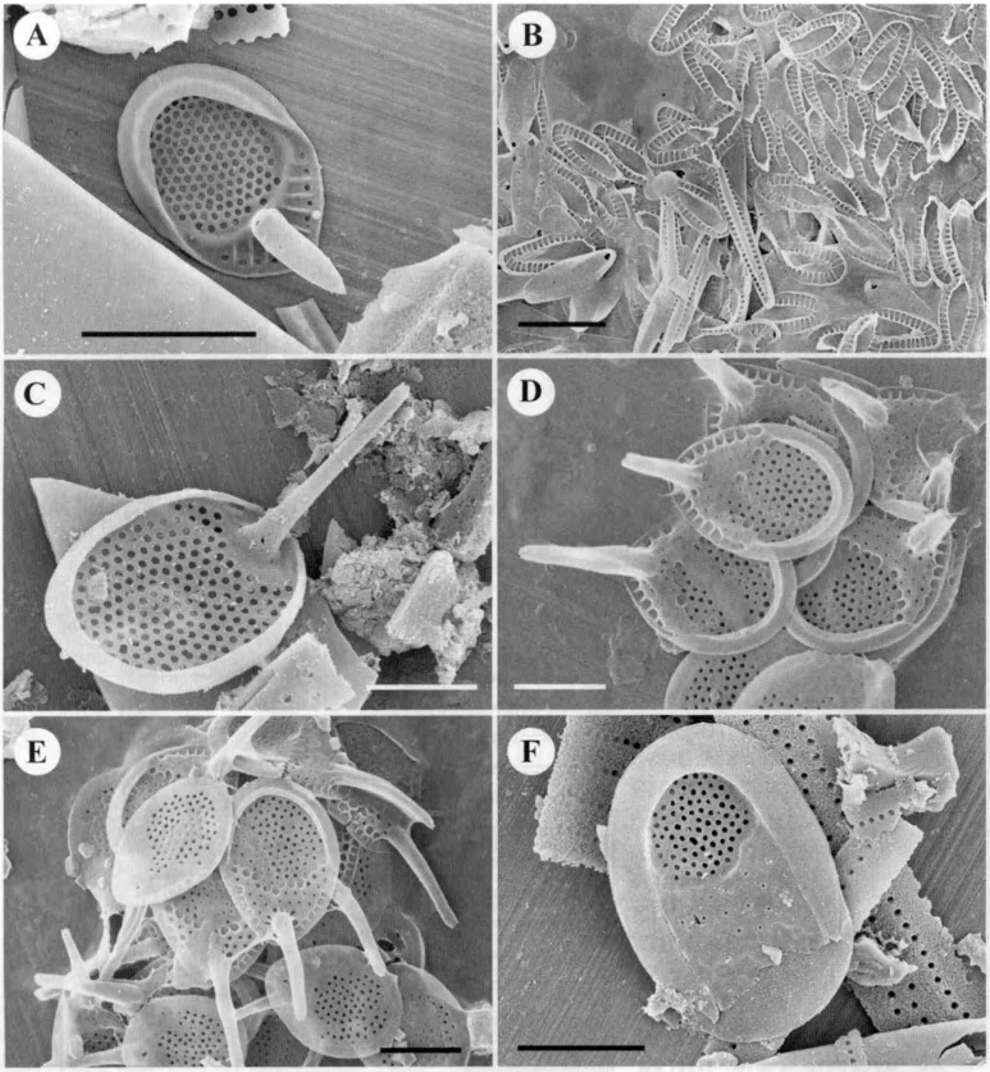

Fig. 6. Scaled chrysophytes from Cape Cod. A. Isolated scale of *Synura echinulata* f. *leptorrhabda.* Scale bar = 2 μm. B. Remains of a cell of *Synura petersenii.* Scale bar = 5 μm. C. Isolated scale of *Synura sphagnicola.* Scale bar = 1 μm. D–E. Scales of *Synura spinosa*. Scale bars = 2 μm. F. Spineless scale of *Synura uvella.* Scale bar = 2 μm.

Fig. 5. Scaled chrysophytes from Cape Cod. A–B. Whole cell (A) and close-up of the anterior region (B) of *Mallomonas tonsurata.* Scale bar for A = 5 μm and 2 μm for B. C. Isolated scale of *Mallomonas torquata* f. *simplex.* Scale bar = 1 μm. D. Remains of a cell of *Paraphysomonas vestita.* Scale bar = 5 μm. E. Remains of cells from *Spiniferomonas bilacunosa* (left) and *Spiniferomonas coronacircumspina* (right). Scale bar = 5 μm. F. Remains of a cell of *Spiniferomonas coronacircumspina*. Scale bar = 2 μm. G. Remains of a cell of *Spiniferomonas takahashii.* Scale bar = 2 μm. H. Remains of a cell of *Spinif-eromonas trioralis.* Scale bar = 2 μm.

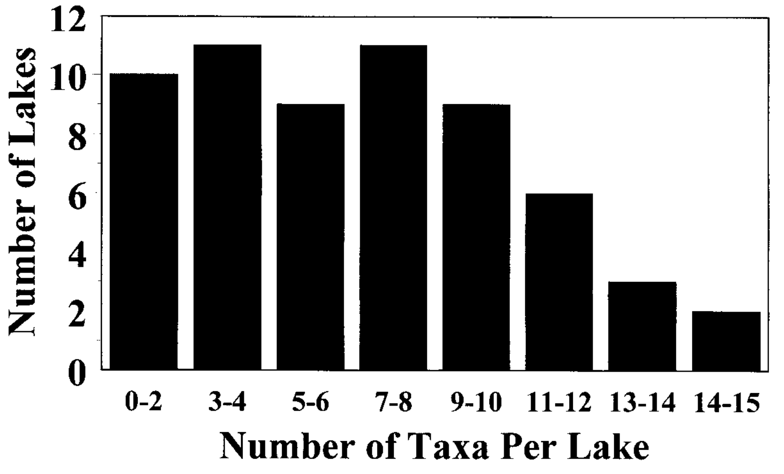

Fig. 7. The number of taxa of scaled chrysophytes found per lake for 60 waterbodies on Cape Cod.

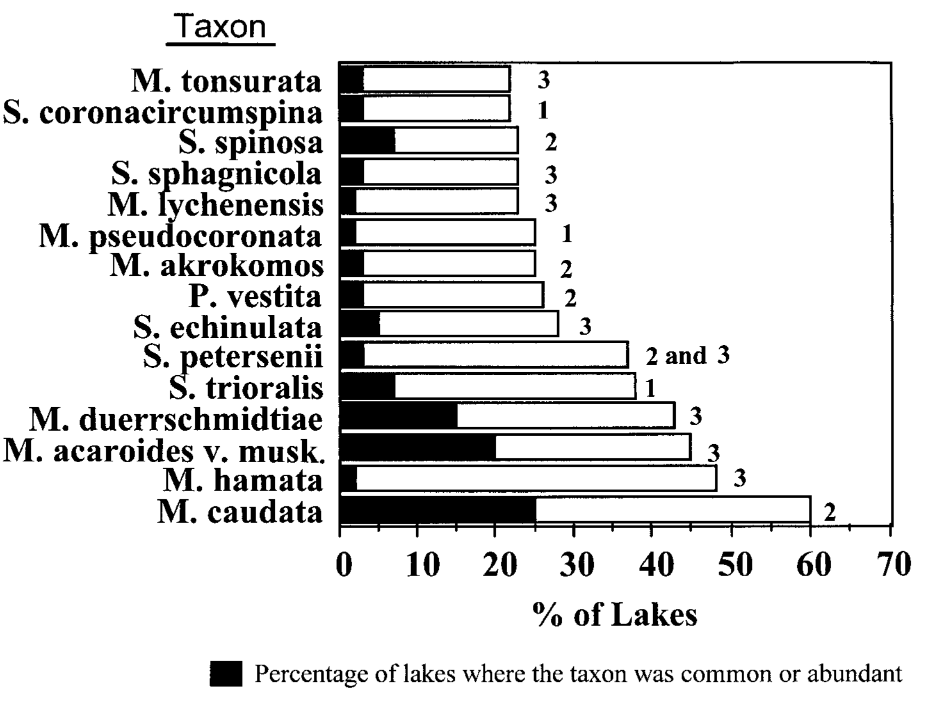

Fig. 8. The percentages of lakes containing the fifteen most abundant species of scaled chrysophytes found in Cape Cod lakes. The darkened portion of each bar represents the percentage of the lakes where an organism was common or abundant, and the open portion the percentage where the organism was rare or very rare. The numbers denote the geographic region that each taxon was most abundant in. Key: 1 = the Bicep; 2 = the Elbow; 3 = the Forearm. See text for more details.

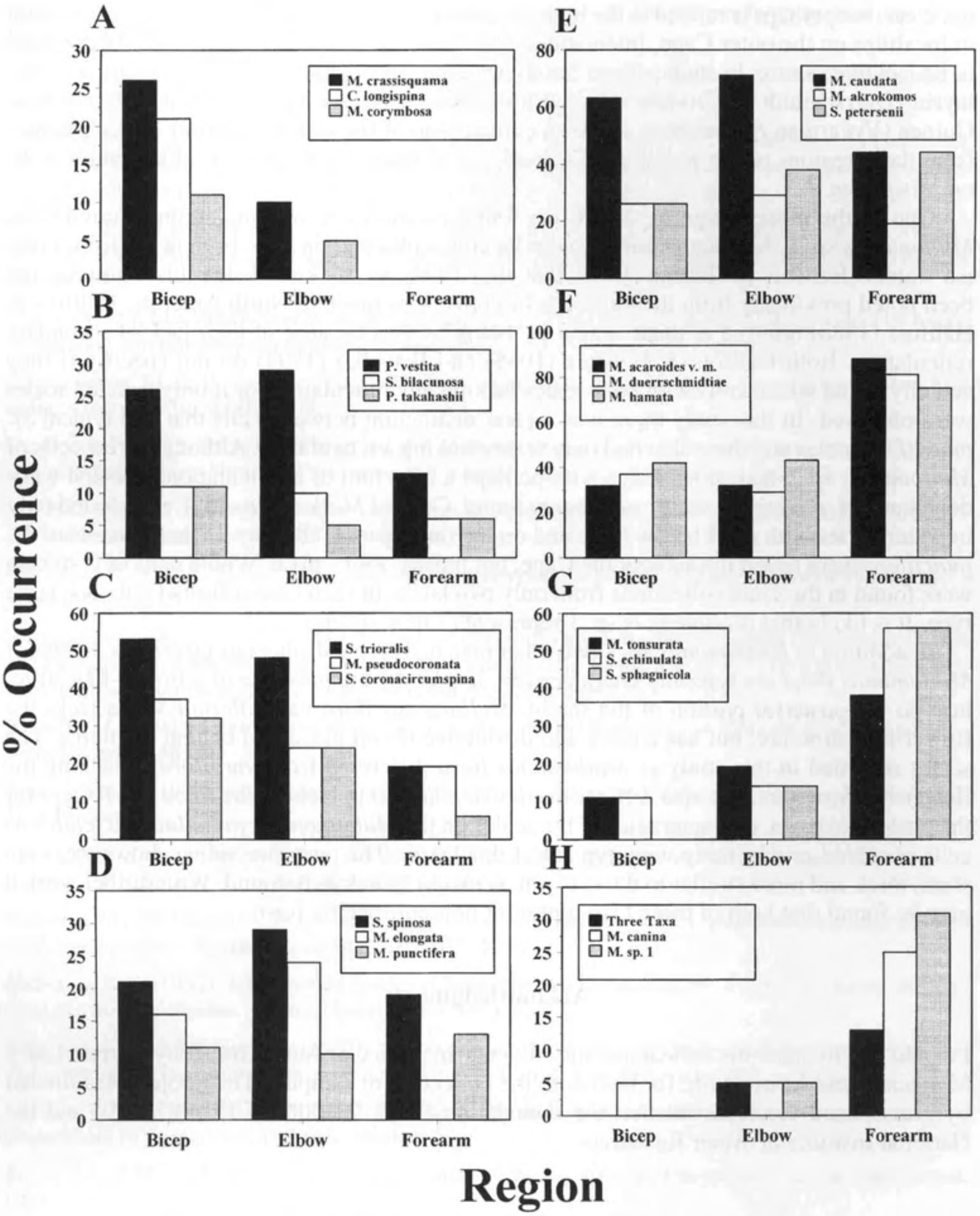

Fig. 9. The percent occurrences for 26 species of scaled chrysophytes in waterbodies on Cape Cod according to geographic region. Organisms in panels A, B and C denote taxa that become less abundant with distance from the mainland out onto the peninsula. Organisms in panels D and E denote taxa that are more or less evenly distributed in waterbodies across the peninsula. Organisms in panels F, G and H denote taxa that become more abundant with distance from the mainland out onto the peninsula.

not clear, but perhaps is related to the high concentrations of sodium, chloride and magnesium in localities on the outer Cape. Interestingly, *Mallomonas crassisquama* also has been found to be lacking, or rare, in studies from South America (Dürrschmidt 1982), Australia and Malaysia (Dürrschmidt & Croome 1985), China (Kristiansen & Tong 1989) and Papua New Guinea (Vyverman & Cronberg 1993). A comparison of the water chemistry of waterbodies from these regions of the world would clearly be of interest regarding the distribution of *M. crassisquama*.

One of the most intriguing organisms found on the Cape was the taxon referred to as *Mallomonas* sp. 1. Although similar scales lacking a reticulation have been noted from Finnish waters (Hällfors & Hällfors 1988, Ikävalko 1994), to my knowledge this taxon has not been noted previously from the hundreds of collections made in North America. Hällfors & Hällfors (1988) referred to these scales as "blank" scales because of their lack of secondary reticulation. Both Hällfors & Hällfors (1988) and Ikävalko (1994) do not specifiy if they actually found whole cells with only scales lacking any reticulation, or if only isolated scales were observed. In this study there was a clear distinction between cells that had typical *M. punctifera* scales and those that had only scales lacking a reticulation. Although a few cells of *Mallomonas* sp. 1 had some scales with perhaps a faint hint of a reticulation, true and well-developed *M. punctifera* scales were never found. Cells of *Mallomonas* sp. 1 were found only in waterbodies with a pH below 6 located on the outer part of the Cape, whereas cells of *M. punctifera* were found throughout the Cape, but mostly above pH 6. Whole cells of both taxa were found in the same collections from only two lakes; in each case cells had only one scale type. It is likely that *Mallomonas* sp. 1 represents a new species.

In addition to *Mallomonas* sp. 1 two other taxa had atypical siliceous coverings. Scales of *Mallomonas flora* are typically characterized, in part, by the presence of a flower-like structure on the posterior portion of the shield. *Mallomonas flora* var. *palermii* Vigna lacks the flower-like structure, but has a thick and distinctive rib on the shield behind the dome. The scales recorded in this study as *Mallomonas flora* differered from var. *flora* in lacking the flower-like structure, but also differed from var. *palermii* in lacking the thick rib. Except for the posterior spines, characteristics of the scales on the *Mallomonas cyathellata* var. *chilensis* cells observed in this study were typical of this taxon. The posterior spines, however, were short, thick and more similar to those of var. *kenyana* Wujek & Asmund. With further work it may be found that both of these taxa represent new subspecific forms.

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