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Miami, Florida

DIATOM-BASED PALEOLIMNOLOGICAL RECONSTRUCTION OF
QUATERNARY ENVIRONMENTS IN A FLORIDA SINKHOLE LAKE

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To: Dean Kenneth Furton
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This dissertation, written by Amanda Kay Quillen, and entitled Diatom-Based Paleolimnological Reconstruction of Quaternary Environments in a Florida Sinkhole Lake, having been approved in respect to style and intellectual content, is referred to you for judgment.

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DEDICATION

I dedicate my dissertation to my husband, Greg Maschek. I could not have done this without him.

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ABSTRACT OF THE DISSERTATION
DIATOM-BASED PALEOLIMNOLOGICAL RECONSTRUCTION OF
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by

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Despite lake sensitivity to climate change, few Florida paleolimnological studies have focused on changes in hydrology. Evidence from Florida vegetation histories raise questions about long-term hydrologic history of Florida lakes, and a 25-year limnological dataset revealed recent climate-driven effects on Lake Annie. The objectives of this research are (1) to use modern diatom assemblages to develop methods for reconstruction of climatic and anthropogenic change (2) to reconstruct both long-term and recent histories of Lake Annie using diatom microfossils.

Paleoenvironmental reconstruction models were developed from diatom assemblages of various habitat types from modern lakes. Plankton and sediment assemblages were similar, but epiphytes were distinct, suggesting differences in sediment delivery from different parts of the lakes. Relationships between a variety of physical and chemical data and the diatoms from each habitat type were explored. Total phosphorus (TP), pH, and color were found to be the most relevant variables for reconstruction, with sediment and epiphyte assemblages having the strongest relationships to those variables, six calibration models were constructed from the combination of these habitat types and

environmental variables. Reconstructions utilizing the weighted averaging models in this study may be used to directly reveal TP, color, and pH changes from a sediment record, which might be suggestive of hydrologic change as well.

These variables were reconstructed from the diatom record from both a long-term (11,000 year) and short-term (100 year) record and showed an interaction between climate-driven and local land-use impacts on Lake Annie. The long-term record begins with Lake Annie as a wetland, then the lake filled to a high stand around 4000 years ago. A period of relative stability after that point was interrupted near the turn of the last century by subtle changes in diatom communities that indicate acidification. Abrupt changes in the diatom communities around 1970 AD suggest recovery from acidification, but concurrent hydrologic change intensified anthropogenic effects on the lake. Diatom evidence for alkalization and phosphorus loading correspond to changes seen in the limnological record.

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1 INTRODUCTION

Understanding the mechanisms driving environmental fluctuations over time is imperative as we face a future of accelerated global climate change. Environmental transformations caused by both natural and anthropogenic processes leave evidence in the fossil record. Paleoecological reconstructions provide the information necessary to elucidate climate patterns of the past, allowing us to interpret modern ecosystems in a historical context and make predictions about the future. Deep sinkhole lakes in Central Florida offer unique opportunities for paleoecological studies because of their age and excellent preservation of sediments (Watts 1980; Watts and Hansen 1988, 1994). Although pollen records from these lakes have resolved some Holocene climate patterns by documenting changes in vegetation communities, the hydrologic consequences of climate fluctuations to lake ecosystems have been relatively unexplored in Florida.

Evidence from reconstructions of vegetation history raises questions about the long-term hydrologic history of Florida lakes, and a 25-year limnological dataset has revealed recent climate-driven effects on Lake Annie, a deep sinkhole lake in South Central Florida (Gaiser et al. 2009). Diatoms have previously been used to uncover information about hydrologic change, providing evidence for a "hydrologic threshold" that was exceeded throughout the Southeast during the mid-Holocene, resulting in the stabilization of lakes and wetlands near their modern hydrologic levels (Gaiser et al. 2001). Florida diatoms are also sensitive to anthropogenic sources of change, especially relating to acidification (Sweets 1992) and nutrient increases (Brenner et al. 1999; Brenner et al. 1996; Deevey et al. 1986).

The first goal of this research is to use modern diatom assemblages to develop methods suitable for reconstructing long-term and recent climatic and anthropogenic change. To accomplish this goal, three objectives will be explored. The first objective is to utilize assemblages from different habitat types to provide a resource for paleolimnological reconstruction of wetland versus lake conditions. The next objective is to discover the relationships between diatom assemblages and a variety of physico-chemical variables, especially those that may be related to changes in water delivery to the lakes. The final objective is to construct predictive models of the most relevant variables using diatom assemblages from different habitat types. These objectives are focused on in Chapter 2.

Chapter 3 addresses the second goal of this research, the reconstruction of both long-term and recent histories of Lake Annie using diatom microfossils. Quantitative and qualitative inferences of long-term and recent changes in the lake will be interpreted from diatom assemblages using models and autecological data derived from Chapter 2 and the literature. Raw count data and environmental data from Chapters 2 and 3 will be available through the Florida Coastal Everglades Long Term Ecological Research (FCE LTER).

The concluding goal of this research is to present a diatom flora for Highlands County, Florida lakes. Diatom taxa discussed in chapters 2 and 3 are presented here for comparison with other Florida diatom research. Photographs and literature references for each taxa are provided.

2 DIATOM BASED MODELS TO PREDICT COLOR, pH, AND TOTAL PHOSPHORUS FROM MULTIPLE HABITAT TYPES IN SINKHOLE LAKES FROM HIGHLANDS COUNTY, FLORIDA, U.S.A

Abstract

Models for paleoenvironmental reconstructions were developed from diatom assemblages of three different habitat types (epiphytes, plankton, and sediments) from 46 lakes on the Lake Wales Ridge in Central Florida. Plankton and sediment assemblages were similarly comprised, but epiphyte assemblages were distinct from those in the sediments, suggesting differences in sediment delivery from different parts of the lakes. A discriminant function analysis was performed to exploit assemblage differences for the purpose of predicting whether an unknown sample came from an epiphytic or planktonic habitat. Relationships between a variety of physical and chemical data and the diatoms from each habitat type were explored. Total phosphorus (TP), pH, and color were found to be the most desirable variables for reconstruction, with sediment and epiphyte assemblages having the strongest relationships to those variables. Six weighted averaging models were constructed from the combination of these habitat types and environmental variables. Reconstructions utilizing the discriminant function and weighted averaging models in this study may be used to directly reveal TP, color, and pH changes from a sediment record that might be suggestive of local or regional changes in climate, land-use and water quality.

Keywords: diatoms, sinkhole lake, Lake Wales Ridge, weighted averaging, prediction model, transfer function, color, nutrients, pH

Introduction

There are nearly 8,000 lakes in Florida, the majority of which are seepage lakes with little overland inflow or outflow (Brenner et al. 1990). Lacking significant overland inputs and outputs, water depth in Florida seepage lakes directly reflects the amount of local rainfall and height of the water table. Lakes are tightly tied to the seasonal and yearly variability in rainfall that is common to Florida, hence water levels are typically *astatic*, or very irregular (Brenner et al. 1990). Changes in precipitation are reflected as changes in lake level with little or no lag (Deevey 1988). If fluctuations in water delivery to a lake trigger chemical and biotic responses that are retained in the sediments, reconstruction of past water level fluctuations may be possible. Paleolimnological reconstruction of hydrologic variability can put current fluctuations into a long-term context, enabling improved future climate projections.

Diatoms can be used as both direct and indirect proxies for changes in water depth (Wolin and Duthie 2001). Associations of diatom species with different aquatic communities can be used directly to infer water level in a lake by noting changes in the ratio of planktonic to non-planktonic species (Cawley et al. 2002; Kingston et al. 1983; Wilson et al. 1997). It is vital that the bathymetry of the lake is taken to account in this type of reconstruction, as the shape and size of the littoral zone will change differently with depth depending on the shape of the basin (Stone and Fritz 2004). In some cases, weighted averaging (WA) models have been developed to relate diatom assemblages directly to depth (Yang and Duthie 1995) and hydroperiod (Gaiser et al. 1998).

Diatoms respond to a variety of chemical variables, allowing for their use in indirect reconstructions of water depth, depending upon how increased precipitation and

water depth affect lake chemistry. Changes in salinity can indicate fluctuating water levels in closed basin lakes as decreased water volume concentrates solutes (Fritz et al. 1999). Drying can result in a release of nutrients from the sediments in some lakes resulting from decreased flushing (Rippey et al. 1997), but often the main source of nutrients is from the surrounding landscape (Webster et al. 2008), with increased precipitation leading to increased nutrient loading. Diatom-inferred pH changes have also been interpreted as signals of a change in water level, with the direction of change being dependent upon the source of water to a given lake (Wolin and Duthie 2001). In Florida, already acidic precipitation reacts with CO₂ in the soil to further drive down groundwater pH (Kindinger et al. 1999), therefore a decrease in diatom-inferred pH might be interpreted as a signal of increased precipitation. Increased precipitation might also deliver more acidic dissolved organic carbon (DOC) to a lake, which acts as a weak buffer to small changes in pH, resulting in a delayed, then abrupt, decline in pH (Tropea et al. 2007).

Human impacts can confound pH and nutrient related reconstructions of water depth as increased acid rain deposition from industry and elevated nutrient input from agriculture may subjugate evidence of natural climate change. Florida diatom assemblages have been used extensively to reconstruct anthropogenic pH (Sweets 1992) and nutrient (Brenner et al. 1999; Brenner et al. 1996; Deevey et al. 1986) changes. Depth reconstructions using pH and nutrient inferences can only be accomplished if the natural pH and nutrient fluctuations associated with water level change can be differentiated from human sources of variation in these variables. Sedimentary records predating human influence in the region of interest can aid in this endeavor (Brenner et

al. 1995; Brenner et al. 1993). Inferences of pH and nutrient changes are the primary applications of diatoms in Florida sediments because of the strength of their association with these variables (Whitmore 1989), therefore finding additional evidence of water depth change that is not confounded by either or both of these variables could be difficult.

Evidence from the examination of a 22-year limnological dataset from Lake Annie (one of the lakes sampled in this study) revealed that increased input of colored dissolved organic matter (CDOM) and reduced visibility is associated with increased rainfall and water table height because of expanded associations with wetlands surrounding the lake (Gaiser et al. 2009). Diatom calibration models have been successfully calculated for DOC concentration (Ruhland and Smol 2002; Schonfelder et al. 2002), color (Korsman and Birks 1996; Korsman and Segerstrom 1998; Miettinen et al. 2005; Ramstack et al. 2003), and transparency (i.e., Secchi disc depth, (Dixit and Smol 1994). A model incorporating one of these variables could be used in conjunction with nutrient and pH models to indirectly reconstruct water level in Lake Annie using diatoms.

The goal of this research is to use diatom assemblages to develop methods suitable for reconstruction of long-term and recent climatic and anthropogenic change. To accomplish this goal, three objectives will be explored. My first objective is to utilize assemblages from different habitat types to provide a resource for paleo-reconstruction of wetland versus lake conditions. The next objective is to discover the relationships between diatom assemblages and a variety of physico-chemical variables, especially those that may be related to changes in water delivery to the lakes. The final objective is

to construct predictive models of the most relevant variables using diatom assemblages from different habitat types.

Study area

The 46 solution lakes sampled for this study are located along the Lake Wales Ridge (LWR), the southernmost portion of the Central Florida ridges and uplands ecoregion (Griffith et al. Undated). The LWR is a 200-mile long line of relict coastal beach sands overlying limestone bedrock, peppered by hundreds of lakes formed by karst processes (White 1970). All of the study lakes are located in Highlands County, on the southernmost portion of the LWR (Figure 1). Candidate lakes were chosen from those with water chemistry data available from the volunteer lake monitoring program, Florida LAKEWATCH (LAKEWATCH 2004). The list of lakes was then narrowed on the basis of depth, color, pH, and total phosphorus (TP) concentration that could have conceivably been experienced by Lake Annie at any time in the past. Emphasis was placed upon finding lakes with a wide range of color and maximum depth.

The climate of Highlands County is humid and subtropical. Seasonal variation is characterized by a warm wet season from June to September and a cool dry season from October to May. Rainfall averages 126 cm per year, with about 60% of that falling during the summer. The vegetation of the area is dominated by Florida scrub habitat, growing on acidic, sandy soils, however no more than 20% of the original extent of this habitat remains, the rest having been developed for citrus agriculture and residences (Christman and Judd 1990). A few of the lakes sampled for this study were located in an area with more or less pristine surroundings, but most were impacted in some way by development.

Methods

Diatom sampling and processing

Diatom samples were collected from all lakes during a two-week period in September 2003. At the deepest point in each lake, sediment samples were collected from the sediment-water interface using an Ekman dredge, and approximately the top 1cm of sediment was saved for analysis. On the same day, living diatoms were qualitatively sampled from each lake. Plankton was collected in each lake using a 20- μ m mesh plankton net, and a periphyton or epiphyton sample was collected from the littoral zone of each lake, taking care to sample proportionately from the different epiphytic habitats representative of each lake.

Organic material was removed from each sample by successively boiling in 30% H_2O_2 and 70% HNO_3 . After allowing the diatoms to settle, the acidic water was repeatedly decanted and the beaker refilled with distilled water until a neutral pH was achieved. Subsamples of cleaned material were dried onto 0.1-mm thick glass coverslips, which were permanently fixed with Naphrax[®] mounting medium onto glass slides. The number of diatom valves (including fragments) were counted in random, measured transects on one slide from each sample at 750x magnification on a Nikon E600 compound microscope. At least 500 diatom valves were identified to the species level using standard literature. Digital photographs were recorded for each species using a Sony CCD camera fitted to the microscope.

Physical and chemical data

The primary source of environmental data was Florida LAKEWATCH (LW), a program using trained volunteers to collect samples that are later analyzed by professionals (LAKEWATCH 2004). Using volunteers allows for more frequent monitoring and the inclusion of far more water bodies than could ordinarily be examined, while maintaining a high level of data quality (Canfield et al. 2002). Data from the Southwest Florida Water Management District (unpublished data) and the United States Geological Survey (USGS 2008) was averaged with the LW data when available. Details of the methods used to perform chemical analyses of samples can be found in (LAKEWATCH 2004).

All values for each variable were averaged daily, then monthly, then quarterly. After values for Total Phosphorous (TP), Total Nitrogen (TN), Chlorophyll A (ChlA), Transparency (Secchi), and Color were averaged quarterly, values for years between 2000 and 2003, with at least two quarters represented, were averaged yearly, then the available years were used to calculate the lake average. Alkalinity (Alk), pH, and Specific Conductivity (SpC) were measured at less regular intervals, therefore lake averages for these data represent measurements taken on one to four different days between 1995 and 2003. Values for maximum depth (Zmax), surface area (SA), mean depth (Z), percent area covered with aquatic vegetation (PAC), percent of lake's volume filled with vegetation (PVI), average emergent plant biomass (AEPB), average floating-leaved plant biomass (AFLPB), average submersed plant biomass (ASPB), and average width of emergent and floating-leaved zone (AWEFLZ) were taken together for each lake on one to six days between 1994 and 2003.

Data analysis

Exploration of pattern in the species data

To reduce noise in the species data, I omitted those taxa present in only 1 lake and those with a maximum abundance less than 0.5% throughout all samples. Species data were square root transformed to reduce the impact of dominant taxa on the analyses. To compare the three habitat types (sediment, epiphytes, and plankton) to each other, an ANOSIM test was performed to reveal the degree to which the sample types differed (Clarke and Gorley 2006). Indicator species analysis (Dufrêne and Legendre 1997) was used to find taxa indicative of the two living habitat types, plankton and epiphytes. I also performed a discriminant function analysis with leave-one-out cross-validation on these live assemblages to determine if I can predict habitat membership in unknown assemblages.

To compare diatom assemblages both between habitat types and among lakes, I used non-metric multidimensional scaling (NMDS) (Kruskal and Wish 1978) with the Bray and Curtis (1957) dissimilarity metric. This NMDS was employed because it does not assume a relationship between environmental and species data, does not result in distortions of the ordination space, and NMDS is capable of accommodating the coefficient most appropriate for species abundance data, Bray-Curtis. I used the slow and thorough autopilot mode in PC-Ord (McCune and Mefford 1999), which employs a Monte Carlo randomization test to determine the number of dimensions necessary, above which no significant reduction of stress occurs.

Relating species data to environmental variables.

A joint plot was constructed for each habitat (epiphytes, plankton, and sediments) separately to observe relationships between the diatom communities and the environmental variables. The length and direction of the environmental vectors are determined by the maximum correlation of each variable with the site similarities. Only environmental variables with high correlations to diatom community site scores will be chosen for development of calibration models.

Models of environmental predictions

Weighted averaging (WA) regression was used to develop models to predict environmental conditions based upon estimates of species optima and tolerances. The tolerances were adjusted based upon the effective number of occurrences of each taxon. Bootstrapping (1000 runs) was used to estimate the RMSE of prediction for each calibration set. Because greatest accuracy for the variables being reconstructed is desired at the ends of the available spectra, classical deshrinking was used (Birks et al. 1990) to reduce shrinking of the range of inferred values. Bootstrap-estimated values for each model were plotted against observed values for each lake, and the linear relationship was observed for significance and strength. Plots of residuals from each regression were also examined for significance, as any relationship detected in the residuals might indicate bias in the model.

Effects of other environmental variables.

Environmental variables were transformed to approximate a normal distribution (Table 1). Pearson correlation analysis was employed to test for independence among all

measured environmental variables. Residuals from each WA model were plotted against each of the measured environmental variables, and a Pearson correlation analysis was performed. I visually inspected these plots, as any type of relationship (linear or otherwise) might indicate bias.

Results

Patterns in the environmental data

Although the 46 sampled lakes reside very close together and are situated on similar substrates, they varied greatly in depth, surface area, and water chemistry (Tables 1 and 2). The ranges of values for TP (4.9-114.9 µg/L) and color (3.1-168.8 Pt-Co units) were large, but most values occurred at the lower end of these gradients (averaging 21.3 µg/L and 25.6 Pt-Co units, respectively). The range of pH values (5.45-8.16) included both acidic and alkaline sites, with an average (6.94) near neutral.

There were many correlated environmental variables (Table 3). Total Phosphorus was highly correlated with chlorophyll a, Secchi transparency, color, maximum depth, and average depth, and pH was highly correlated with alkalinity and specific conductivity (Table 3).

Variation in the species data

I identified 297 taxa from approximately 55 genera in the plankton, epiphytes, and sediments. There were many dominant taxa with 16 taxa present in at least 50% of samples and 15 taxa with over 30% abundance in any sample. The five taxa that met both of these criteria were *Cyclotella stelligera*, *Brachysira microcephala*, *Aulacoseira ambigua*, *Aulacoseira granulata*, and *Achnanthydium minutissimum*. The dominant

species differed by sample type. *Cyclotella stelligera*, *Aulacoseira ambigua*, and *Aulacoseira granulata* were most abundant in the sediment. In addition to those three species, *Brachysira microcephala* also dominated in the plankton. *Brachysira microcephala* and *Achnantheidium minutissimum* were most abundant in the epiphytes. Taxa present in at least 50% of lakes differed by sample type with 12 in epiphyte samples, 16 taxa in plankton, and 28 taxa in sediments. There were many rare species in the dataset, with 64 species present in only one sample, and 87 species with a maximum abundance of less than 0.5%.

The indicator species analysis identified 14 taxa significantly associated with epiphytic habitats and nine taxa significantly associated with the plankton. All but one of the dominant taxa were recognized as indicators of one group or the other, with *Achnantheidium minutissimum* dominating epiphyte assemblages, and *Cyclotella stelligera*, *Aulacoseira ambigua*, *Aulacoseira granulata* dominating planktonic assemblages. *Brachysira microcephala*, dominant in both the epiphytes and plankton, did not emerge as an indicator for either group.

Bray-Curtis similarity scores (reported as a proportion of similarity between samples) revealed differences in diatom assemblages among habitats. Similarity between all samples averaged 0.31. If only a single habitat type is taken into account, similarity between sites was higher, averaging 0.36, 0.35, and 0.41 for epiphytes, plankton, and sediments, respectively. Maximum similarity between plankton sites and sediment sites was 0.69, with epiphytes only slightly higher at 0.70. Taking all samples together, 31 lakes had similarity greater than 0.50 between at least two of their habitats, mostly between sediment and plankton habitats. Maximum similarity between any two samples

was 0.74. Eight pairs of samples scored a similarity of zero, with only two of those pairs being from the same sample type (both epiphyte pairs). Minimum similarity between plankton site pairs and between sediment site pairs was 0.04 and 0.07, respectively.

The NMDS including all three habitat types was captured in three dimensions, but only axes 1 and 3 were visually informative (Figure 2). The NMDS clearly shows a separation of the plankton and sediment samples from the epiphytes. The ANOSIM supports this evidence, indicating that plankton and sediment samples are the most similar ($R=0.138$, $p<0.001$), while epiphytes differ the most from sediment ($R=0.515$, $p<0.001$), then plankton ($R=0.359$, $p<0.001$). Axis 1 represents the gradient between sediment and plankton samples, with much overlap. Axis 3 represents the gradient between epiphytes and the other habitats, with less overlap. The wide gradient exhibited by the epiphyte samples reflects the lower minimum similarity values between epiphyte sample pairs. Discriminant function analysis correctly predicted epiphytic samples 60.9% of the time, and planktonic samples 65.2% of the time.

Relationships between species and environmental data

A two-dimensional NMDS ordination displayed differences between lake epiphyte assemblages (Figure 3a). A biplot illustrated the relationships between environmental variables and NMDS site scores (Table 4). Similarity among sites was most highly correlated with pH ($r^2 = 0.74$, $p < 0.01$), closely followed by correlated variables alkalinity ($r^2 = 0.63$, $p < 0.01$) and specific conductivity ($r^2 = 0.48$, $p < 0.01$). These three vectors vary along a similar axis. Color ($r^2 = 0.37$, $p < 0.01$) varies in the opposite direction close to this axis, while the TP ($r^2 = 0.35$, $p < 0.01$) vector is further away from the pH axis, though not completely perpendicular to it.

Plankton (Figure 3b) and sediment (Figure 3c) ordinations both necessitated display in three dimensions, with the two most informative axes presented in each figure. The two biplots were very similar with nearly the same relationship among vectors, though environmental vector correlations for TP and associated variables were strongest with the sediment samples (Table 4). Total Phosphorus was the variable most highly correlated with compositional similarity ($r^2 = 0.80$, $p < 0.01$), followed by correlated variables Secchi transparency ($r^2 = 0.68$, $p < 0.01$), color ($r^2 = 0.67$, $p < 0.01$), and maximum depth ($r^2 = 0.54$, $p < 0.01$). These variables, along with average depth ($r^2 = 0.41$, $p < 0.01$) and chlorophyll a ($r^2 = 0.52$, $p < 0.01$), are represented on the same axis, while the opposing axis incorporates variation in pH ($r^2 = 0.48$, $p < 0.01$), specific conductivity ($r^2 = 0.47$, $p < 0.01$), and alkalinity ($r^2 = 0.38$, $p < 0.01$).

For plankton, alkalinity had the strongest correlation with diatom assemblage similarity ($r^2 = 0.65$, $p < 0.01$), and varied along with associated variables pH ($r^2 = 0.61$, $p < 0.01$) and specific conductivity ($r^2 = 0.51$, $p < 0.01$). These correlations were higher than their respective values for the sediment samples. Color ($r^2 = 0.64$, $p < 0.01$), Secchi transparency ($r^2 = 0.55$, $p < 0.01$), TP ($r^2 = 0.52$, $p < 0.01$), maximum depth ($r^2 = 0.45$, $p < 0.01$), and average depth ($r^2 = 0.42$, $p < 0.01$) varied nearly perpendicular to the alkalinity axis, as with the sediments, though correlations with plankton site scores were lower than with the sediments. I chose to create WA models for TP, pH, and color, using epiphyte (Table 6) and sediment (Table 5) diatom assemblages.

Weighted averaging (WA) models

The WA TP model created with sediment samples estimated optima between 6.6 $\mu\text{g/L}$ (*Fragilaria parasitica*) and 69.2 $\mu\text{g/L}$ (*Aulacoseira granulata* morphSmall), with an

average of 18.7 µg/L. Sediment WA adjusted tolerances for TP ranged between 1.0 µg/L (*Pinnularia brauniana*) and 3.4 µg/L (*Brachysira neoacuta*), averaging 1.8 µg/L, with 75% of species having an adjusted tolerance below the mean. The epiphyte TP model exhibited a wider range of optima from 6.2 µg/L (*Pinnularia gibba*) to 93.3 µg/L (*Navicula* sp. 5), averaging 21.9 µg/L. The epiphyte WA adjusted tolerances for TP varied between 1.1 µg/L (*Cocconeis fluviatilis*) and 4.0 µg/L (*Stenopterobia curvula*), with an average adjusted tolerance of 1.9 µg/L and 53% of species tolerances falling below the mean.

The WA color model created with sediment samples estimated optima between 4.1 Pt-Co units (*Cymbella kolbei* v. *angusta*) and 107.8 Pt-Co units (*Aulacoseira granulata*, small form), with an average of 16.8 Pt-Co units. Sediment WA adjusted tolerances for color ranged between 1.3 Pt-Co units (*Tabellaria flocculosa* v. *linearis*, small form) and 5.3 Pt-Co units (*Staurosira venter*, medium form), averaging 2.5 Pt-Co units, with 57% of species having an adjusted tolerance below the mean. The epiphyte color model exhibited a wider range of optima from 4.2 Pt-Co units (*Cymbella kolbei* v. *angusta*) to 152.2 Pt-Co units (*Navicula* sp. 5), averaging 28.8 Pt-Co units. The epiphyte WA adjusted tolerances for TP varied between 1.1 Pt-Co units (*Rhopalodia gibba*) and 7.3 Pt-Co units (*Stenopterobia curvula*), with an average adjusted tolerance of 2.6 Pt-Co units and 59% of species tolerances falling below the mean.

The sediment WA pH model optima ranged from 6.1 (*Frustulia pseudomagaliesmontana*) to 7.8 (*Nitzschia frustulum*), averaging 6.9. The sediment WA adjusted tolerances for pH varied from 0.02 (*Cyclostephanos* cf. *dubius*) to 1.29 (*Pinnularia brauniana*), with an average adjusted tolerance of 0.62 and 66% of species

falling below the mean. The epiphyte pH model also covered a wider range of optima from 5.7 (*Pinnularia microstauron*) to 7.9 (*Encyonema* (?) sp. 2), averaging 6.6. Epiphyte WA adjusted tolerances for pH ranged between 0.03 (*Caloneis bacillum*) and 0.96 (*Pinnularia gibba*), averaging 0.42, with 52% of species having an adjusted tolerance below the mean.

Prediction of environmental conditions

Sediment samples revealed a stronger relationship between diatom assemblages and TP ($r^2 = 0.85$) or color ($r^2 = 0.76$), while epiphytic assemblages show a tighter association with pH ($r^2 = 0.87$) (Table 7 and Figure 4). Residuals showed no linear trend in any of the models.

Effects of other environmental variables

Visual inspection of residuals from the epiphyte WACAL models showed that TP and color residuals were significantly correlated to pH (Table 8). Visual inspection of residuals from the sediment WACAL models did not reveal any obvious relationships with other environmental variables, however other significant linear relationships were revealed by the Pearson's correlation analysis (Table 8). Despite these trends in the residuals, creation of weighted averaging partial least squares (WA-PLS) models did not significantly reduce standard errors.

Discussion

Diatom autecology

The flora of Highlands County overlaps with floras found throughout the Eastern United States, including those from South Carolina (Gaiser and Johansen 2000), New

York (Camburn and Charles 2000), and Massachusetts (Siver et al. 2005). The flora is similar to that of (Whitmore 1989), though nomenclatural changes and the lack of photographs make comparisons difficult. The autecology of three of the five most abundant taxa (*Cyclotella stelligera*, *Brachysira microcephala*, *Aulacoseira ambigua*) are indicative of acidic to circumneutral, oligotrophic to mesotrophic conditions (Siver et al. 2005). *Aulacoseira granulata*, also a circumneutral species, is tolerant of mesotrophic to eutrophic conditions (Whitmore 1989). The average nutrient and pH values of the lakes in this study are mesotrophic and circumneutral. *Achnanthydium minutissimum* is a commonly occurring diatom with a wide range of tolerances (Siver et al. 2005). *Cyclotella stelligera*, *Aulacoseira ambigua*, and *Achnanthydium minutissimum* are known to have wide DOC tolerances (Camburn and Charles 2000).

Effect of habitat type

The most desirable calibration set for a paleolimnological reconstruction is one that boasts the greatest overlap in taxa throughout the core. While a given calibration set may not provide the strongest relationship to a given environmental variable, the increased species overlap between model and fossil taxa will result in a stronger reconstruction (Overpeck et al. 1985). The logic of sampling multiple habitats in this study is to increase species overlap by utilizing more than one calibration set, which is especially important if planning to reconstruct a particularly long sediment history. Deep sinkhole lakes in Florida have sediment histories dating back to the Pleistocene, when water tables were much lower than today, leaving all but the deepest lake basins dry (Grimm et al. 1993; Watts and Hansen 1994). The taxa found in the basal sediments of these old lakes may overlap more with an epiphytic reference set because the reduced

water level could have produced wetland conditions in the basin, resulting in the sedimentation of more epiphytic species. Changes in percentages of diatoms of different life-forms, especially planktonic versus epiphytic species, have been used extensively in qualitative water depth reconstructions (Wolin and Duthie 2001).

The high ANOSIM value between plankton and sediment samples suggests interchangeability in their use in calibration and reconstruction. Physico-chemical variable correlations with site scores may be higher with sediment samples over plankton samples due to integration of variable fluctuations over time. Plankton samples reflect the live assemblage present at the time of sampling, but variables were not measured on the exact day of sampling in this study. It may be desirable to use plankton samples for studies where variables are measured concurrent with collection of the diatom sample, although plankton may also integrate some level of change over time, and a single observation of a variable is undesirable if it can be avoided. If using averaged variable data taken over several seasons or years, sediment diatom samples are preferred, as they represent an integration of the taxa that were present over an extended time period.

The higher ANOSIM value between plankton and epiphyte samples versus sediment and epiphyte samples may be reflecting the differences between diatom life and death assemblages. The lower overlap between epiphyte and sediment assemblages also implies that not very much littoral material gets sedimented in the deepest part of the lake. An increase in epiphytic species in a sinkhole lake history suggests either a more dominant littoral zone or a shift of the zone toward the deepest part of the lake, either suggesting shallower water depth. Likewise, discriminant function analysis could reflect

a change to shallower depth if the function predicts that an assemblage is epiphytic rather than planktonic.

Choice of model variables

Florida lake sediments have the potential to reveal thousands of years of climate variability. While TP and pH have fluctuated significantly in recent years due to anthropogenic influences, they may also be capable of revealing important climatic variation that took place prior to human settlement. Color appears to correlate directly with higher lake levels, and its correlations with TP (positive) and pH (negative) may suggest that all three variables are changing for similar reasons. Increased color and TP can both be explained by increased allochthonous input (Webster et al. 2008) resulting from increased overland water flow. Decreased pH can also be explained as precipitation increases delivery of acidic rainwater and groundwater.

Increased rainfall cannot directly be accounted for spatially in the modern dataset because precipitation data for individual lakes is not available. The range of resultant consequences of increased precipitation exhibited in the lake set is due to differences in the "watershed" of each lake. Some are less impacted by increased water flow due to isolation from wetlands or other natural sources of color and nutrients. Similarly, proximity to homes, agriculture, or other human activity can alter the chemistry of the lake. Since the diatoms are responding directly to the consequences of climatic change (increased TP and color, pH decrease) and not to the climate driver itself (increased rainfall), down core reconstructions are still relevant to changes in precipitation for a particular lake.

For these lakes, a direct depth model was not developed for reconstruction. Although maximum (Z_{max}) and average (Z) depth has a significant relationship with sediment site scores, color and TP are negatively correlated with depth. One explanation for this relationship is that deeper lakes might be more connected to groundwater, receiving a greater portion of their inflow from below ground versus over land. If the source of the colored organic material and nutrients is above ground, such as a connection to a nearby wetland or drainage ditch, this might account for these relationships. I suspect that increased water flow into a lake causes increased color and nutrients regardless of the depth of the lake, though the change may be less dramatic in lakes with smaller watersheds or fewer connections to wetlands.

Measurements of pH were correlated with alkalinity and specific conductivity. It is not clear if the relationship between pH and specific conductivity is causative or coincidental. Gaiser et al (2009) found that decreases in the groundwater level are associated with increased conductivity, likely due to concentration of ions in shallower water. In this study, pH is positively correlated with conductivity, but also positively correlated with depth. Acid deposition may be confounding this relationship, and it will be interesting to reconstruct pH histories from before human industrialization.

Conclusion

It is important to use as many lines of evidence as possible to draw conclusions about historic hydrologic fluctuations. The complement of tools supplied in this study can be implemented together to provide evidence for diatom-based changes in hydrology from the sediments of Florida sinkhole lakes. Depending upon the variable of interest

and the sampling strategy of said variable, sampling of different habitats within a lake might improve the quality of reconstructions.

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Table 1: Physico-chemical characteristics of the 46 lakes included in this study with their minimum, maximum, mean, standard deviation, and transformation used for analysis.

Abbreviation	Variable	Units	N	Minimum	Maximum	Mean	Standard deviation	Transformation
TP	Total Phosphorus	µg/L	46	4.9	114.9	21.3	20.5	log
TN	Total Nitrogen	µg/L	46	355	2912	861	597	log
ChlA	Chlorophyll a	µg/L	46	1.5	73.4	14.0	15.2	log
SECCHI	Transparency	m	46	0.39	6.74	2.32	1.62	4thrt
COLOR	Color	Pt-Co units	45	3.1	168.8	25.6	37.3	log
SpC	Specific Conductance	µS/cm	45	41.8	371.2	153.4	69.3	log
pH	pH	standard units	45	5.45	8.16	6.94	0.65	NONE
ALK	Alkalinity	mg/L	45	0.10	42.26	13.14	11.45	4thrt
Zmax	Maximum depth	m	46	1.83	22.00	8.38	5.36	log
SA	Surface area	hectares	46	0.8	2316.5	198.7	443.7	log
Z	mean depth	m	32	1.57	11.20	4.37	2.51	log
PAC	Percent area covered with aquatic vegetation	%	29	0.0	59.0	20.0	13.9	sqrt
PVI	Percent of lake's volume filled with vegetation	%	29	0.00	31.60	4.94	5.99	4thrt
AEPB	Average emergent plant biomass	kg wet wt/m2	33	0.30	10.20	3.62	2.11	NONE
AFLPB	Average floating-leaved plant biomass	kg wet wt/m2	33	0.00	19.30	1.75	3.49	4thrt
ASPB	Average submersed plant biomass	kg wet wt/m2	33	0.00	4.10	0.91	1.07	sqrt
AWEFLZ	Average width of emergent and floating-leaved zone	ft	33	0.27	120.98	29.05	27.19	4thrt

Table 2: Mean values of physico-chemical variables for each of the 46 lakes sampled in this study.

Abbreviation	Lake Name	TP	TN	ChlA	SECCHI	COLOR	SpC	pH	ALK	Zmax	SA	Z	PAC	PVI	AEPB	AFLPB	ASPB	AWEFLZ
AD	Adelaide	14.3	529	8.8	1.77	30.3	91.0	6.32	2.89	5.18	44.0	3.20	32.0	4.20	5.00	0.20	2.70	19.51
AN	Annie	6.8	378	5.4	2.50	44.4	41.8	5.95	0.10	19.80	34.8	9.10						
AP	Apthorpe	11.3	1263	7.8	2.35	18.9	209.2	7.05	14.90	7.50	88.6	4.20	34.0	3.80	6.10	0.70	0.90	19.26
BN	Bonnet	38.4	1353	53.8	0.72	21.8	246.9	7.62	34.98	3.05	108.5				5.60	5.20	0.00	25.76
CA	Carrie	42.9	895	24.8	0.69	137.3	94.8	6.76	13.32	4.27	26.3	2.70	13.0	3.70	2.30	1.10	0.00	11.80
CH	Chilton	18.4	525	18.0	1.84	5.8	73.8	6.81	2.74	7.01	10.5	3.90	8.0	2.10	4.00	0.10	0.40	15.24
CL	Clay	11.6	520	5.1	3.08	7.6	165.1	6.87	6.55	7.92	201.5	2.90	59.0	7.10	4.40	4.70	2.80	30.02
CR	Crews	17.0	533	7.5	1.05	34.9	67.6	5.77	2.42	5.49	25.5	2.70	10.0	3.80	3.90	2.70	0.20	39.59
DA	Damon	16.2	397	5.8	1.49	8.3	220.0	6.15	2.67	5.40	114.1							
DE	Denton	4.9	2590	1.5	6.74	3.5	291.2	7.90	39.15	15.85	27.9	7.60	13.0	2.00	2.50	0.00	1.20	18.78
DN	Dinner	9.3	597	5.0	2.81	5.5	183.3	7.87	31.23	9.75	170.0	4.70	44.0	15.10	3.20	0.10	1.70	19.93
EP	Eagle Pond	27.8	1232	27.7	1.03	17.0	80.0	6.63	5.40	1.83	0.8	1.70	36.0	31.60	5.30	0.00	0.00	3.17
FR	Francis	15.0	643	9.8	2.00	11.1	165.8	6.90	6.38	6.10	238.8	3.60	16.0	2.80	3.70	1.50	2.00	32.92
GR	Grassy	8.6	653	2.7	4.00	10.7	155.5	7.60	20.07	4.00	209.2	2.10	46.0	10.60	0.50	0.30	0.60	15.97
HE	Henry	17.2	576	12.3	1.86	13.8	162.4	7.01	7.78	5.80	25.9							
HI	Hill	10.1	400	6.5	2.05	32.5	54.4	5.45	2.69	6.10	29.9	2.70	29.0	5.50	0.50	0.70	2.00	21.61
HU	Huntley	19.1	535	4.3	2.00	12.8	160.0	6.45	4.16	4.57	431.4				5.80	1.20	0.10	13.41
IS	Isis	5.5	2773	1.8	6.22	3.1	203.5	7.31	16.87	19.50	21.4	8.50						
JA	Jackson	18.2	437	5.0	2.49	10.3	116.2	6.61	4.19	7.01	1704.6	4.40	18.0	1.80	4.20	0.80	3.10	120.98
JC	Josephine Center	74.3	998	22.3	0.54	135.9	81.8	6.22	7.13	1.83	98.9	1.57	16.2	5.40	5.58	4.70	0.40	101.03
JE	Josephine East	54.8	994	35.0	0.74	87.7	104.9	6.52	6.59	2.44	254.4	1.64	11.5	3.50	4.30	3.32	0.67	57.80
JU	June	11.2	531	7.4	2.54	10.6	168.1	7.07	8.83	10.36	2316.5	4.40	20.6	3.18	3.70	0.63	0.30	27.43
JW	Josephine West	114.9	1021	20.4	0.47	168.8	80.6	6.30	7.85	2.13	173.6	1.61	12.7	5.23	5.65	3.83	0.30	73.76
LB	Little Bonnet	23.1	1613	39.4	0.49	14.6	263.3	7.79	29.10	4.80	34.0							
LE	Lelia	13.4	719	17.8	1.54	12.7	178.6	7.39	20.80	10.00	66.8							
LG	Little Grassy	10.0	605	4.7	3.15	5.0	177.8	7.28	19.90	5.50	3.8							
LJ	Little Jackson	56.5	1117	46.9	0.81	26.8	139.4	7.55	10.92	6.71	55.4	3.80	11.0	2.20	4.30	1.40	0.10	20.70
LL	Lillian	11.1	872	7.9	2.55	6.6	144.3	7.35	17.40	12.80	13.0	6.60	10.0	1.00	3.30	0.10	1.50	15.51
LO	Lotela	13.3	520	3.9	2.27	4.7	142.9	6.44	3.53	11.58	279.2				10.20	0.70	0.30	47.85
LR	Little Redwater	23.8	641	16.9	1.16	29.0	89.2	6.42	4.33	6.00	133.1							
LT	Letta	20.8	355	6.4	1.13	5.5	185.0	6.16	2.24	2.65	193.4							
LW	Little Redwater 2	21.5	1350	21.0	0.90	5.0	270.5	7.48	20.90	6.10	8.1	3.10	24.0	4.40	1.90	1.70	0.10	10.67
MC	McCoy	5.4	1077	1.6	4.72	3.4	185.1	7.82	22.87	18.90	16.2	8.40						
OL	Olivia	10.2	513	6.9	2.66	9.0	95.6	7.12	7.79	12.80	36.0	5.50	24.0	3.20	4.50	0.90	4.10	18.29
PE	Pearl	7.2	655	2.0	5.29	5.0	147.1	6.77	10.72	10.91	26.7							
PI	Pioneer	8.5	597	4.3	3.35	5.8				9.45	34.4				1.10	0.00	2.00	7.62
PL	Placid	14.6	440	9.2	2.38	12.1	111.1	6.94	3.27	15.54	1298.7	6.70	2.0	0.30	1.80	0.20	0.30	64.53
PM	Persimmon	34.0	2912	73.4	0.39	20.6	371.2	7.89	34.45	3.66	17.8	2.15	12.0	3.20	1.80	0.25	0.00	8.47
RB	Red Beach	16.5	723	11.0	1.09	44.3	82.3	6.54	4.90	5.49	136.0	2.90	3.0	0.70	2.10	0.90	0.10	28.04
RD	Redwater	23.1	1384	32.1	0.75	20.9	229.2	7.66	26.64	5.18	29.5	2.60	26.0	5.60	2.10	0.50	0.20	12.04
SE	Sebring	46.3	656	9.5	0.66	68.1	95.9	6.17	2.72	3.05	205.6	2.00	24.0	6.50	3.30	0.10	0.70	31.27
SI	Sirena	7.7	441	2.9	5.29	5.3	167.8	6.85	7.65	11.50	61.9							
TR	Trout	18.3	504	12.6	2.26		128.2	6.32	1.87	9.14	55.4	5.20	14.0	3.70	5.90	19.30	0.30	22.86
TU	Tulane	6.5	574	3.0	5.14	4.5	129.8	7.65	20.70	22.00	36.0							
VE	Verona	12.9	435	7.3	4.31	5.4	119.1	7.57	27.48	20.00	15.8	11.20	0.0	0.00	0.50	0.00	0.00	2.68
VI	Viola	8.2	523	4.2	3.66	4.5	231.5	8.16	42.26	8.84	24.3	6.60	12.0	1.00	0.30	0.00	0.90	0.27
	Minimum	4.9	355	1.5	0.39	3.1	41.8	5.45	0.10	1.83	0.8	1.57	0.0	0.00	0.30	0.00	0.00	0.27
	Maximum	114.9	2912	73.4	6.74	168.8	371.2	8.16	42.26	22.00	2316.5	11.20	59.0	31.60	10.20	19.30	4.10	120.98
	Mean	21.3	861	14.0	2.32	25.6	153.4	6.94	13.14	8.38	198.7	4.37	20.0	4.94	3.62	1.75	0.91	29.05
	Standard deviation	20.5	597	15.2	1.62	37.3	69.3	0.65	11.45	5.36	443.7	2.51	13.9	5.99	2.11	3.49	1.07	27.19
	Count	46	46	46	46	45	45	45	45	46	46	32	29	29	33	33	33	33

Table 3: Pearson correlation matrix of transformed environmental variables measured in 46 lake set (* and ** indicate significant correlations at the $p \geq 0.05$ and the $p \geq 0.01$ level, respectively).

Variable	TP	TN	ChlA	SECCHI	COLOR	SpC	pH	ALK	Zmax	SA	Z	PAC	PVI	AEPB	AFLPB	ASPB
TN	0.200															
ChlA	0.813**	0.325*														
SECCHI	-0.890**	-0.225	-0.884**													
COLOR	0.761**	0.075	0.605**	-0.739**												
SpC	-0.182	0.484**	-0.027	0.129	-0.536**											
pH	-0.271	0.501**	-0.001	0.266	-0.508**	0.718**										
ALK	-0.139	0.599**	0.046	0.150	-0.349*	0.718**	0.898**									
Zmax	-0.794**	-0.165	-0.612**	0.779**	-0.633**	0.091	0.326*	0.123								
SA	0.147	-0.331*	-0.087	-0.054	0.180	-0.012	-0.225	-0.275	-0.038							
Z	-0.738**	-0.150	-0.611**	0.784**	-0.682**	0.189	0.386*	0.157	0.964**	-0.067						
PAC	-0.169	0.048	-0.195	0.062	-0.062	0.154	-0.026	0.009	-0.277	0.023	-0.392*					
PVI	0.173	0.230	0.126	-0.295	0.224	-0.053	-0.195	-0.132	-0.609**	-0.140	-0.670**	0.827**				
AEPB	0.305	0.005	0.108	-0.218	0.153	-0.113	-0.375*	-0.418*	-0.203	0.207	-0.273	0.246	0.371*			
AFLPB	0.470**	-0.040	0.357*	-0.453**	0.532**	-0.129	-0.429*	-0.381*	-0.329	0.356*	-0.388*	0.139	0.185	0.468**		
ASPB	-0.477**	-0.389*	-0.551**	0.490**	-0.267	-0.117	-0.117	-0.192	0.320	0.234	0.207	0.455*	0.116	-0.017	-0.062	
AWEFLZ	0.369*	-0.118	0.038	-0.259	0.426*	-0.333	-0.522**	-0.507**	-0.212	0.653**	-0.317	0.002	0.076	0.456**	0.591**	0.218

Table 4: Correlation coefficients (R^2) for linear correlations of environmental variables with sediment (S), plankton (P), and epiphyte (E) NMDS site scores (* and ** indicate significant correlations at the $p \geq 0.05$ and the $p \geq 0.01$ level, respectively).

Variable	S	P	E
TP	0.798 **	0.524 **	0.352 **
TN	0.086	0.171 *	0.187 *
ChlA	0.519 **	0.299 *	0.052
SECCHI	0.684 **	0.549 **	0.167 *
COLOR	0.668 **	0.638 **	0.373 **
SpC	0.472 **	0.511 **	0.482 **
pH	0.48 **	0.609 **	0.737 **
ALK	0.382 **	0.65 **	0.632 **
Zmax	0.535 **	0.451 **	0.181 *
SA	0.202 *	0.172 *	0.188 *
Z	0.414 **	0.419 **	0.238 *
PAC	0.159	0.052	0.011
PVI	0.071	0.018	0.042
AEPB	0.102	0.286 *	0.227 *
AFLPB	0.295 *	0.179	0.241 *
ASPB	0.139	0.079	0.029
AWEFLZ	0.194	0.293 *	0.445 **

Table 5 (two pages): Diatom taxa relative abundances, WA optima and tolerances, number of occurrences, and effective number of occurrences (Hill's N2) for sediment TP (46 lakes), Color (45 lakes), Zmax (46 lakes), and pH (45 lakes) models (* denote significant ($p < 0.05$) planktonic indicators defined by the indicator species analysis).

Taxon name	Freq. of occ.	Hill's N2	TP		Color		pH	
			Optimum ($\mu\text{g/L}$)	Tolerance ($\mu\text{g/L}$)	Optimum (Co Units)	Tolerance (Co Units)	Optimum	Tolerance
<i>Achnanthes exigua</i>	13	9.3	24.4	2.2	20.4	3.1	7.12	0.71
<i>Achnanthes</i> sp. 2	8	7.5	26.7	2.3	26.7	2.6	6.92	0.76
<i>Achnanthes</i> sp. 5	3	2.9	15.6	1.2	6.2	1.5	6.30	0.15
<i>Achnantheidium minutissimum</i>	35	29.8	14.6	1.8	9.7	2.0	7.25	0.51
<i>Actinella punctata</i>	4	3.7	10.0	1.5	19.8	2.7	6.23	0.73
* <i>Amphora ovalis</i>	28	25.5	18.4	2.1	13.3	2.7	7.14	0.59
* <i>Asterionella ralfsii</i> v. <i>americana</i>	7	6.5	12.3	1.5	19.7	2.4	6.36	0.72
* <i>Aulacoseira ambigua</i>	39	29.3	19.8	2.0	15.6	2.7	6.95	0.58
* <i>Aulacoseira herzogii</i>	37	25.7	18.0	1.8	16.9	2.8	6.81	0.72
<i>Aulacoseira</i> sp. 1	15	12.8	35.9	1.9	41.3	3.3	6.67	0.58
<i>Aulacoseira</i> cf. <i>perglabra</i>	4	3.7	20.5	1.3	12.7	2.2	6.89	0.53
<i>Aulacoseira crassipunctata</i>	8	5.2	19.3	1.5	14.5	2.5	7.02	0.57
* <i>Aulacoseira granulata</i>	25	17.2	30.8	1.9	33.2	3.2	6.66	0.58
<i>Aulacoseira granulata</i> , small form	2	1.8	69.2	1.7	107.8	1.6	6.45	0.16
<i>Aulacoseira lacustris</i>	11	8.6	22.8	1.6	18.1	1.7	7.07	0.61
<i>Aulacoseira nygaardii</i>	21	14.9	13.0	1.8	11.2	2.6	7.01	0.72
<i>Aulacoseira tenella</i>	29	21.2	21.8	2.2	23.2	3.1	6.76	0.67
<i>Brachysira brebissonii</i>	26	19.1	10.9	1.6	10.2	2.4	6.91	0.73
<i>Brachysira neoacuta</i>	2	1.9	13.6	3.4	8.9	3.1	7.16	0.90
<i>Brachysira neoexilis</i>	38	25.4	13.7	1.8	10.6	2.1	7.24	0.60
<i>Brachysira procera</i>	7	6.2	16.1	1.8	9.7	2.3	7.27	0.63
<i>Brachysira serians</i>	8	6.2	10.5	1.7	15.6	2.7	6.52	1.00
<i>Caloneis bacillum</i>	6	5.9	27.3	2.2	21.0	2.9	6.85	0.66
<i>Caloneis lewisii</i> v. <i>inflata</i>	9	8.2	18.3	1.9	13.9	2.0	7.13	0.51
<i>Chamaepinnularia</i> sp. 1	2	2.0	8.4	1.3	19.0	3.1	6.57	0.83
<i>Cocconeis placentula</i>	9	7.4	30.9	2.5	23.8	3.8	6.94	0.61
<i>Cyclotephanos</i> cf. <i>dubius</i>	2	1.9	20.7	1.2	17.3	1.8	6.44	0.02
* <i>Cyclotella meneghiniana</i>	26	22.0	19.4	2.3	16.3	3.0	7.12	0.56
* <i>Cyclotella stelligera</i>	46	36.3	12.8	1.8	9.2	2.4	7.10	0.59
<i>Cymbella cuspidata</i>	7	6.6	17.8	1.6	14.1	1.9	6.98	0.64
<i>Cymbella kolbei</i> v. <i>angusta</i>	4	3.8	6.7	1.3	4.1	1.3	7.68	0.26
<i>Cymbella peraffinis</i>	7	6.8	7.5	1.5	4.5	1.3	7.67	0.24
<i>Diademsis confervacea</i>	5	4.9	49.0	2.1	55.2	3.6	6.72	0.52
<i>Diploneis parma</i>	4	3.9	15.4	1.3	7.6	1.5	6.60	0.38
<i>Encyonema</i> cf. <i>carina</i>	3	2.9	11.5	1.4	10.0	1.3	7.17	0.41
<i>Encyonema evergladianum</i>	13	10.5	10.1	1.7	8.1	2.2	7.54	0.74
<i>Encyonema</i> cf. <i>gaeumannii</i>	11	9.1	14.1	1.4	15.9	2.4	6.47	0.64
<i>Encyonema sublanceolatum</i>	5	3.9	10.0	1.3	17.3	2.5	6.35	0.90
<i>Encyonema minutum</i>	26	20.7	13.6	1.7	9.2	2.0	7.13	0.48
<i>Encyonema neogracile</i>	36	30.3	14.9	1.7	12.6	2.5	6.83	0.65
<i>Encyonema silesiacum</i>	32	25.0	15.3	2.0	11.2	2.5	7.21	0.53
<i>Encyonopsis microcephala</i>	13	11.8	13.8	2.0	8.3	2.1	7.75	0.25
<i>Encyonopsis subminuta</i>	25	20.5	10.3	1.6	7.4	1.8	7.38	0.45
<i>Epithemia adnata</i>	3	2.9	11.7	1.3	6.5	1.5	7.53	0.47
<i>Eunotia carolina</i>	34	22.0	12.5	1.8	12.0	2.5	7.01	0.74
<i>Eunotia veneris</i>	16	9.6	13.1	1.8	19.1	2.6	6.42	0.79
<i>Eunotia</i> cf. <i>faba</i>	41	31.1	17.5	1.9	13.7	2.7	6.94	0.62
<i>Eunotia</i> cf. <i>minor</i>	18	13.1	13.6	2.0	10.7	2.2	7.52	0.39
<i>Eunotia diodon</i>	5	3.9	10.5	1.6	19.0	2.8	6.20	0.69
<i>Eunotia exigua</i> , morph 2	10	6.6	14.2	1.8	23.4	1.8	6.37	0.91
<i>Eunotia formica</i>	35	23.9	14.6	1.7	13.4	2.5	6.79	0.74
<i>Eunotia incisa</i>	20	15.4	13.3	1.9	14.4	2.7	6.78	0.54
<i>Eunotia intermedia</i>	20	16.6	13.4	1.6	12.5	2.3	6.90	0.76
<i>Eunotia</i> sp. 2	6	5.5	33.2	2.0	24.0	4.9	6.94	0.65
<i>Eunotia</i> sp. 3	5	4.2	10.9	1.5	9.3	2.5	7.34	0.41
<i>Eunotia naegeli</i>	12	11.3	15.0	1.7	16.3	2.4	6.55	0.70
<i>Eunotia pectinalis</i>	14	12.1	17.7	1.4	15.0	2.2	6.63	0.56
<i>Eunotia yanomami</i>	16	12.2	18.9	1.9	18.8	2.5	6.68	0.72
<i>Eunotia yanomami</i> , long form	9	8.4	14.5	1.6	19.7	2.3	6.37	0.69
* <i>Eunotia zasuminensis</i>	16	12.5	22.7	2.2	25.7	3.1	6.58	0.50
<i>Fragilaria bidens</i>	10	9.1	31.2	1.7	25.2	2.9	7.14	0.69
<i>Fragilaria capucina</i> v. <i>gracilis</i>	6	5.1	15.4	1.4	7.8	1.5	6.86	0.53
<i>Fragilaria</i> cf. <i>nanana</i>	32	26.9	16.5	1.8	11.6	2.4	7.10	0.63
<i>Fragilaria</i> sp. 3	9	8.5	15.0	1.5	13.5	1.9	6.68	0.29
<i>Fragilaria parasitica</i>	3	2.6	6.6	1.4	4.4	1.4	7.66	0.42

Table 5 continued

<i>Frustulia crassinervia</i>	24	21.5	14.4	1.9	13.4	2.6	6.78	0.69
<i>Frustulia krammeri</i>	35	26.9	16.5	1.9	14.8	2.7	6.73	0.70
<i>Frustulia pseudomagaliesmontana</i>	8	4.3	12.2	1.6	21.3	2.3	6.10	0.76
<i>Frustulia saxonica</i>	39	27.7	17.1	1.8	15.6	2.6	6.71	0.68
<i>Gomphonema affine</i>	2	1.8	12.8	1.9	9.5	3.3	7.39	1.02
<i>Gomphonema auritum</i>	25	21.1	15.8	1.7	10.4	2.0	7.05	0.55
<i>Gomphonema gracile</i>	10	9.4	26.5	1.7	18.4	2.7	7.17	0.58
<i>Gomphonema gracile</i> , long form	3	2.9	15.2	2.1	10.7	2.0	7.18	0.53
<i>Gomphonema parvulum</i>	8	7.6	29.1	2.2	27.5	3.0	6.72	0.73
<i>Gomphonema camburnii</i>	3	3.0	33.5	2.4	25.4	5.0	7.14	0.80
<i>Kobayasiella madumensis</i>	6	5.5	10.1	1.4	10.3	2.5	6.99	0.67
<i>Navicula capitata</i> var. <i>lueneburgensis</i>	6	5.7	17.7	1.8	13.1	2.9	6.84	0.63
<i>Navicula</i> cf. <i>agrestis</i>	2	1.8	25.9	2.3	17.3	1.6	7.20	0.38
<i>Navicula</i> cf. <i>seminulum</i>	2	2.0	34.2	2.2	26.8	2.4	7.00	0.87
<i>Navicula</i> cf. <i>similis</i>	17	15.1	21.1	2.2	15.4	3.2	6.93	0.61
<i>Navicula constans</i>	10	9.0	17.9	1.5	13.6	2.3	6.91	0.66
<i>Navicula cryptocephala</i>	43	36.4	14.2	1.8	11.4	2.4	6.91	0.68
<i>Navicula protracta</i>	4	3.7	16.3	1.5	14.9	2.2	7.04	0.67
<i>Navicula viridula</i>	4	3.2	10.2	1.4	5.5	1.5	7.78	0.65
<i>Neidium amphigomphus</i>	25	16.7	14.7	1.7	12.1	2.4	6.66	0.83
<i>Neidium ampliatum</i>	13	11.2	16.5	2.2	16.4	3.0	6.67	0.72
<i>Neidium ampliatum</i> , small form	4	3.5	17.6	2.3	9.5	2.2	7.13	0.38
<i>Neidium densestriatum</i>	23	19.3	13.6	1.7	11.6	2.3	6.92	0.76
<i>Nitzschia amphibia</i>	12	9.3	16.9	2.1	10.0	2.2	7.70	0.34
<i>Nitzschia</i> cf. <i>acidoclinata</i>	8	7.6	20.4	2.2	16.0	2.8	7.19	0.48
<i>Nitzschia frustulum</i>	2	1.9	21.8	3.0	12.2	3.1	7.82	0.39
<i>Nitzschia nana</i>	11	10.5	16.0	1.8	8.7	1.9	7.07	0.53
<i>Nitzschia palea</i>	17	15.9	15.7	2.0	11.6	2.5	7.00	0.69
<i>Nitzschia palea</i> v. <i>debilis</i>	17	14.1	24.2	2.2	17.5	3.4	6.72	0.62
<i>Pinnularia amabilis</i>	10	9.4	15.6	2.3	18.1	3.4	6.83	0.89
<i>Pinnularia brauniana</i>	2	1.9	10.0	1.0	14.9	3.8	6.21	1.29
<i>Pinnularia brauniana</i> , morph 2	2	1.9	8.7	1.3	5.0	2.4	7.07	0.36
<i>Pinnularia</i> cf. <i>balatonis</i>	2	1.8	9.0	1.3	14.8	3.1	6.76	0.83
<i>Pinnularia</i> cf. <i>decrescens</i>	31	25.0	15.7	1.7	13.8	2.7	6.80	0.73
<i>Pinnularia gibba</i>	20	17.2	14.1	1.6	11.9	2.4	6.71	0.69
<i>Pinnularia gibbiformis</i>	2	1.8	61.8	1.2	45.5	3.2	7.12	0.94
<i>Pinnularia microstauron</i>	8	7.3	8.6	1.4	9.9	2.8	6.79	0.91
<i>Pinnularia oominensis</i>	3	2.8	16.6	1.8	10.3	1.7	7.66	0.16
<i>Pinnularia schroeterae</i> v. <i>elliptica</i>	2	1.9	11.7	1.3	14.9	2.4	6.79	0.57
<i>Planothidium</i> sp. 1	3	2.8	15.6	1.5	8.2	1.6	7.13	0.46
<i>Planothidium apiculatum</i>	4	3.7	35.3	2.4	29.4	3.1	6.84	0.58
<i>Pleurosigma salinarum</i>	3	2.5	18.0	1.2	7.5	1.6	6.44	0.25
<i>Sellaphora pupula</i>	23	18.5	17.6	1.8	12.6	2.4	7.07	0.60
<i>Stauroneis acidobionta</i>	6	5.6	21.5	1.8	22.8	2.8	6.45	0.69
<i>Stauroneis pachycephala</i>	9	7.9	10.5	1.7	8.5	2.4	7.34	0.47
<i>Stauroneis phoenicenteron</i>	17	16.0	21.1	2.4	17.5	3.4	7.02	0.64
<i>Stauroneis staurolineata</i>	10	8.8	16.8	1.5	14.9	2.1	6.67	0.66
<i>Staurosira venter</i>	18	11.6	31.3	2.2	23.2	3.3	6.97	0.61
<i>Staurosira venter</i> , long form	7	5.8	41.0	2.6	36.4	3.5	6.88	0.57
<i>Staurosira venter</i> , medium form	4	2.6	53.3	3.1	57.9	5.3	6.46	0.26
<i>Staurosira venter</i> , pinched form	4	3.8	25.7	2.5	19.9	3.4	7.03	0.69
<i>Staurosirella pinnata</i>	7	6.5	32.9	2.5	24.4	4.1	7.02	0.66
<i>Staurosirella</i> sp. 2	6	5.1	37.2	2.3	32.3	3.2	7.10	0.72
<i>Stenopterobia curvula</i>	6	5.7	10.6	1.6	11.1	2.5	6.65	0.69
<i>Stenopterobia delicatissima</i>	5	4.3	11.3	1.5	14.6	2.9	6.45	0.72
<i>Surirella biseriata</i>	9	8.4	22.5	1.5	17.2	2.3	6.80	0.73
<i>Surirella cuspidata</i>	13	11.2	12.7	1.7	14.9	2.4	6.60	0.79
<i>Surirella guatemalensis</i>	3	2.5	15.6	1.6	7.3	1.6	6.87	0.95
<i>Surirella linearis</i>	4	3.2	17.2	1.9	12.1	1.7	6.92	0.54
<i>Surirella linearis</i> v. <i>constricta</i>	13	10.5	13.4	1.6	17.2	2.4	6.37	0.83
<i>Synedra acus</i>	12	10.4	20.9	1.9	12.1	1.9	7.46	0.39
<i>Fragilariforma spinulosa</i>	2	2.0	13.6	1.1	12.9	3.4	6.94	0.89
<i>Tabellaria flocculosa</i>	4	3.9	10.5	1.5	14.0	3.1	6.38	0.87
<i>Tabellaria flocculosa</i> v. <i>linearis</i>	20	13.0	16.6	1.8	20.0	2.4	6.54	0.60
<i>Tabellaria flocculosa</i> var. <i>linearis</i> , medium form	9	8.2	14.6	1.8	16.5	2.9	6.65	0.63
<i>Tabellaria flocculosa</i> var. <i>linearis</i> , small form	3	2.7	11.3	1.1	9.0	1.3	7.08	0.23
<i>Thalassiosira</i> cf. <i>visurgis</i>	11	8.4	8.8	1.4	5.9	1.5	7.48	0.59
<i>Thalassiosira</i> sp. 1	5	4.8	42.0	2.1	53.8	2.3	6.72	0.58
<i>Ulnaria ulna</i>	14	13.0	22.4	1.9	17.6	3.1	6.96	0.71
unknown large <i>Pinnularia</i> , broken valves	39	32.5	18.2	2.0	15.0	2.8	6.81	0.70

Table 6 (two pages): Diatom taxa relative abundances, WA optima and tolerances, number of occurrences, and effective number of occurrences (Hill's N2) for epiphyte TP (46 lakes), Color (45 lakes), Zmax (46 lakes), and pH (45 lakes) models (* denote significant ($p < 0.05$) epiphytic indicators defined by the indicator species analysis).

Taxon name	Freq. of occ.	Hill's N2	TP	TP	Color	Color	pH	pH
			Optimum (µg/L)	Tolerance (µg/L)	Optimum (Co Units)	Tolerance (Pt Co Units)	Optimum	Tolerance
<i>Achnanthes cf. delicatula</i>	2	1.5	38.5	1.9	68.1	2.4	6.20	0.10
<i>Achnanthes exigua</i>	12	9.0	19.1	1.9	17.9	2.4	6.83	0.48
<i>Achnanthes exigua v. elliptica</i>	9	6.0	15.1	1.6	13.5	2.2	6.87	0.45
<i>Achnanthes sp. 1</i>	2	2.0	31.6	2.2	30.1	4.5	6.57	0.06
<i>Achnanthes sp. 2</i>	6	4.3	37.2	2.3	57.3	2.7	6.40	0.39
<i>Achnanthes sp. 3</i>	4	3.2	63.6	2.0	110.8	1.7	6.24	0.07
<i>Achnanthes sp. 4</i>	3	2.7	53.0	2.3	101.4	1.9	6.24	0.09
<i>Achnanthes sp. 5</i>	3	2.9	16.4	1.2	6.2	1.4	6.24	0.16
* <i>Achnanthidium minutissimum</i>	39	31.5	15.5	1.8	11.2	2.4	7.11	0.51
<i>Asterionella ralfsii v. americana</i>	4	2.4	10.2	2.0	34.0	1.8	6.04	0.31
<i>Aulacoseira ambigua</i>	14	9.0	28.7	2.2	27.3	3.2	6.65	0.39
<i>Aulacoseira herzogii</i>	12	6.6	24.0	2.1	33.3	2.6	6.17	0.42
<i>Aulacoseira sp. 1</i>	6	4.6	58.7	2.0	89.6	3.0	6.40	0.21
<i>Aulacoseira granulata</i>	16	8.4	44.2	2.0	64.2	3.3	6.50	0.39
<i>Aulacoseira lacustris</i>	3	2.3	18.1	1.2	35.2	1.2	6.06	0.47
<i>Aulacoseira nygaardii</i>	5	4.3	10.9	1.8	19.4	2.6	6.31	0.39
<i>Aulacoseira tenella</i>	11	9.0	28.5	2.7	32.9	4.1	6.47	0.31
<i>Brachysira brebissonii</i>	19	10.9	10.3	1.8	9.6	2.7	6.79	0.48
<i>Brachysira neoexilis</i>	42	35.7	13.8	1.9	11.2	2.4	7.02	0.68
* <i>Brachysira procera</i>	28	21.2	14.5	1.7	12.7	2.3	6.82	0.57
<i>Brachysira serians</i>	3	2.9	9.3	1.4	36.3	1.2	5.87	0.41
<i>Caloneis bacillum</i>	2	2.0	58.7	1.4	96.3	1.6	6.19	0.03
<i>Chamaepinnularia sp. 1</i>	2	2.0	12.2	2.4	36.4	1.4	6.17	0.33
<i>Cocconeis fluviatilis</i>	2	1.7	45.2	1.1	83.7	1.6	6.34	0.41
<i>Cyclotella stelligera</i>	42	31.5	13.8	2.1	10.5	2.9	7.12	0.59
<i>Cymbella kolbei v. angusta</i>	3	1.9	6.4	1.2	4.2	1.2	7.74	0.23
<i>Diademsis confervacea</i>	5	4.6	24.9	1.9	21.4	3.4	6.69	0.54
<i>Encyonema cf. carina</i>	4	3.9	13.3	2.4	8.1	2.5	7.91	0.16
<i>Encyonema evergladianum</i>	16	9.7	11.3	2.1	7.5	2.2	7.72	0.40
<i>Encyonema minutum</i>	22	14.8	13.7	1.8	10.2	2.4	6.78	0.68
<i>Encyonema neogracile</i>	25	15.8	18.7	2.1	22.4	2.9	6.42	0.56
* <i>Encyonema silesiacum</i>	38	30.1	16.5	1.9	11.2	2.4	7.16	0.54
<i>Encyonema silesiacum</i> , "big" form	6	5.7	20.7	2.0	12.2	2.1	7.21	0.57
<i>Encyonema silesiacum</i> , long form	10	9.3	12.0	1.9	8.0	2.0	7.26	0.49
* <i>Encyonopsis microcephala</i>	22	16.7	13.3	2.1	9.2	2.3	7.55	0.47
* <i>Encyonopsis subminuta</i>	27	22.6	11.8	1.8	8.2	2.1	7.37	0.45
<i>Eunotia camelus</i>	5	4.2	27.0	2.7	41.7	5.3	6.41	0.28
<i>Eunotia carolina</i>	19	10.9	13.4	1.7	18.4	2.5	6.64	0.62
<i>Eunotia veneris</i>	13	7.6	16.9	2.3	24.7	3.2	6.44	0.47
* <i>Eunotia cf. faba</i>	33	19.3	21.0	2.1	21.8	3.0	6.73	0.52
<i>Eunotia cf. minor</i>	16	11.3	18.4	2.3	13.7	2.6	7.43	0.46
<i>Eunotia exigua</i> , morph 2	12	10.2	14.3	1.8	22.5	2.1	6.40	0.64
<i>Eunotia flexuosa</i>	2	1.9	62.5	1.4	105.7	1.6	6.20	0.03
<i>Eunotia formica</i>	11	7.8	17.7	2.1	26.0	2.9	6.11	0.30
<i>Eunotia incisa</i>	4	2.8	12.0	1.9	18.3	3.2	6.46	0.38
<i>Eunotia intermedia</i>	18	14.3	15.3	2.2	12.5	3.2	6.64	0.59
<i>Eunotia naegeli</i>	7	4.2	22.3	2.0	28.7	2.3	6.39	0.30
<i>Eunotia pectinalis</i>	8	7.0	30.0	2.9	33.6	4.7	6.37	0.27
<i>Eunotia rabenhorstiana</i>	4	3.8	47.9	2.7	47.6	5.5	6.41	0.50
<i>Eunotia transfuga</i>	3	2.8	38.8	3.2	72.1	2.7	6.28	0.06
<i>Eunotia yanomami</i> , long form	2	1.7	7.6	1.3	40.5	1.2	5.81	0.35
<i>Eunotia zasuminensis</i>	9	7.8	29.1	2.1	29.0	3.9	6.38	0.21
<i>Fragilaria bidens</i>	10	6.0	18.6	1.7	18.9	2.5	6.81	0.50
* <i>Fragilaria capucina v. gracilis</i>	14	9.3	15.1	1.9	10.4	2.3	7.06	0.58
<i>Fragilaria cf. nanana</i>	24	16.3	15.1	1.7	12.6	2.2	6.91	0.58
<i>Fragilaria sp. 2</i>	4	3.5	18.2	1.4	11.7	1.9	7.32	0.41
<i>Fragilaria sp. 3</i>	7	4.6	14.7	1.3	7.3	2.2	6.55	0.55
* <i>Frustulia crassinervia</i>	21	15.6	20.8	2.2	24.3	3.1	6.42	0.41
<i>Frustulia krammeri</i>	13	11.5	15.2	1.7	20.6	2.3	6.25	0.46
<i>Frustulia pseudomagalesmontana</i>	3	2.4	10.2	1.7	39.0	1.2	5.82	0.20
<i>Frustulia saxonica</i>	21	12.1	25.5	2.6	35.6	3.4	6.40	0.53

Table 6 continued

* <i>Gomphonema affine</i>	16	12.8	19.5	2.1	12.6	3.5	6.93	0.56
* <i>Gomphonema auritum</i>	41	28.2	17.3	2.1	13.4	3.0	6.80	0.65
<i>Gomphonema clavatum</i>	8	7.0	21.4	2.4	17.8	3.7	7.03	0.66
<i>Gomphonema coronatum</i>	2	1.9	27.4	1.5	9.2	2.8	7.54	0.09
* <i>Gomphonema gracile</i>	18	13.5	25.3	2.3	23.9	3.5	6.78	0.54
<i>Gomphonema gracile</i> , long form	5	4.9	10.8	1.4	9.9	2.4	7.03	0.38
<i>Gomphonema mexicanum</i>	5	4.0	13.9	1.7	7.4	1.7	6.91	0.67
* <i>Gomphonema parvulum</i>	16	11.4	28.7	1.9	24.9	3.9	6.57	0.46
<i>Gomphonema parvulum</i> v. <i>lagenula</i>	7	6.1	13.7	2.1	13.8	4.1	7.06	0.65
<i>Gomphonema camburnii</i>	3	1.9	47.8	1.2	84.8	1.6	6.30	0.34
<i>Mastogloia smithii</i>	3	2.8	14.0	1.7	12.5	1.2	7.64	0.19
<i>Navicula brasiliana</i>	2	1.9	10.1	1.2	11.9	2.3	7.05	0.42
<i>Navicula</i> cf. <i>similis</i>	11	9.0	15.3	1.7	9.3	1.9	6.80	0.54
<i>Navicula</i> cf. <i>wildii</i>	17	14.8	11.7	1.7	7.1	1.9	7.56	0.45
<i>Navicula cryptocephala</i>	30	22.8	19.3	2.1	18.7	2.9	6.62	0.52
<i>Navicula</i> sp. 4	4	2.5	78.6	2.0	117.0	2.1	6.28	0.09
<i>Navicula</i> sp. 5	2	2.0	93.3	1.4	152.2	1.2	6.26	0.06
<i>Navicula notha</i>	5	4.3	12.0	2.2	30.4	2.6	6.05	0.48
<i>Navicula subrhynchocephala</i>	2	1.9	11.1	1.2	16.0	4.0	5.81	0.70
<i>Navicula</i> sp. 8	2	1.9	17.6	1.1	44.3	2.4	6.40	0.16
<i>Navicula viridula</i>	2	1.7	10.5	1.7	6.8	1.5	6.61	0.42
<i>Neidium amphigomphus</i>	6	5.7	11.5	1.5	15.6	2.9	6.04	0.51
<i>Neidium</i> cf. <i>amphirhynchus</i>	4	3.6	15.2	2.5	15.1	3.5	6.91	0.29
<i>Neidium densistriatum</i>	7	6.0	13.1	1.9	21.6	2.7	6.31	0.67
<i>Nitzschia amphibia</i>	19	11.7	20.6	1.8	14.7	2.7	7.30	0.54
* <i>Nitzschia</i> cf. <i>acidoclinata</i>	20	15.4	14.3	1.6	10.8	2.2	6.95	0.49
<i>Nitzschia</i> cf. <i>capitellata</i>	2	1.6	23.3	1.9	68.1	2.4	6.28	0.10
<i>Nitzschia</i> sp. 3	3	2.9	15.7	1.2	7.3	1.5	6.36	0.24
* <i>Nitzschia nana</i>	21	15.8	23.9	2.2	19.6	3.8	6.49	0.41
<i>Nitzschia palea</i>	17	15.1	17.6	1.7	12.9	2.3	6.63	0.42
<i>Nitzschia palea</i> v. <i>debilis</i>	25	14.1	15.4	2.2	10.6	3.2	6.80	0.66
<i>Nitzschia semirobusta</i>	3	2.7	16.6	2.4	10.1	2.5	7.81	0.40
<i>Pinnularia amabilis</i>	7	6.6	13.9	2.5	27.2	3.2	6.36	0.64
<i>Pinnularia</i> cf. <i>decrescens</i>	5	4.7	16.9	1.5	18.4	2.1	6.10	0.58
<i>Pinnularia gibba</i>	2	1.9	6.2	1.2	14.8	6.5	6.51	0.96
<i>Pinnularia microstauron</i>	2	2.0	8.5	1.3	37.4	1.2	5.68	0.35
<i>Planothidium</i> sp. 2	2	2.0	24.0	2.6	58.1	4.1	6.88	0.21
<i>Rhopalodia gibba</i>	3	2.9	10.4	1.3	5.2	1.1	7.82	0.29
<i>Sellaphora pupula</i>	11	8.6	19.2	1.9	17.7	2.9	6.59	0.54
<i>Staurosira venter</i>	12	9.4	17.3	1.7	10.3	1.8	7.07	0.53
<i>Staurosira venter</i> , long form	4	3.5	19.7	1.5	15.5	2.4	6.65	0.33
<i>Staurosirella pinnata</i>	5	4.3	31.0	2.5	21.4	4.3	6.88	0.64
<i>Stenopterobia curvula</i>	2	1.9	16.4	4.0	15.5	7.3	6.72	0.23
<i>Stenopterobia delicatissima</i>	2	2.0	8.5	1.3	37.4	1.2	5.68	0.35
<i>Stenopterobia delicatissima</i> , morph 2	13	11.8	17.5	2.0	21.0	2.5	6.41	0.57
<i>Surirella linearis</i> v. <i>constricta</i>	2	1.9	14.6	2.0	25.7	1.6	5.88	0.83
<i>Synedra acus</i>	14	8.4	15.8	1.7	10.0	1.8	6.97	0.62
<i>Tabellaria flocculosa</i> v. <i>linearis</i>	7	5.7	13.0	1.6	17.4	2.6	6.25	0.43
<i>Tabellaria flocculosa</i> v. <i>linearis</i> , medium form	9	6.3	18.3	2.3	18.7	4.0	6.30	0.42
<i>Thalassiosira</i> cf. <i>visurgis</i>	8	6.4	10.7	1.5	6.6	1.6	7.28	0.41
<i>Thalassiosira</i> sp. 1	2	1.9	61.3	1.2	103.2	1.4	6.41	0.22
<i>Ulnaria ulna</i>	12	9.9	25.9	1.9	26.1	3.4	6.51	0.33
unknown large <i>Pinnularia</i> , broken valves	10	9.4	19.3	2.6	18.4	3.3	6.67	0.54

Table 7: Summary of the performance of the six WACAL models.

Model	Sample Type	RMSE	RMSEP	r ²	p
logTP	Sediment	0.13	0.16	0.85	<0.0001
	Epiphytes	0.22	0.27	0.66	<0.0001
logColor	Sediment	0.25	0.31	0.76	<0.0001
	Epiphytes	0.31	0.36	0.68	<0.0001
pH	Sediment	0.38	0.48	0.74	<0.0001
	Epiphytes	0.25	0.30	0.87	<0.0001

Table 8: Significant Pearson correlations between WACAL residuals and environmental variables for (a) sediment models and (b) epiphyte models (* and ** indicate significant correlations at the $p \geq 0.05$ and the $p \geq 0.01$ level, respectively).

a.

residual	TP	ChlA	SECCHI	COLOR	SA
TP					0.469**
Color	0.422**		-0.312*		
pH	-0.351*	-0.478**	0.463**	-0.342*	

b.

residual	TN	ChlA	COLOR	SpC	pH	ALK	SA
TP	-0.373*	-0.405**		-0.386**	-0.543**	-0.439**	0.344*
Color	-0.489**	-0.378*		-0.415**	-0.636**	-0.615**	
pH			-0.309*				

Figure 1: Map of Florida showing the location of the 46 sampled lakes in Highlands County (inset) in Florida.

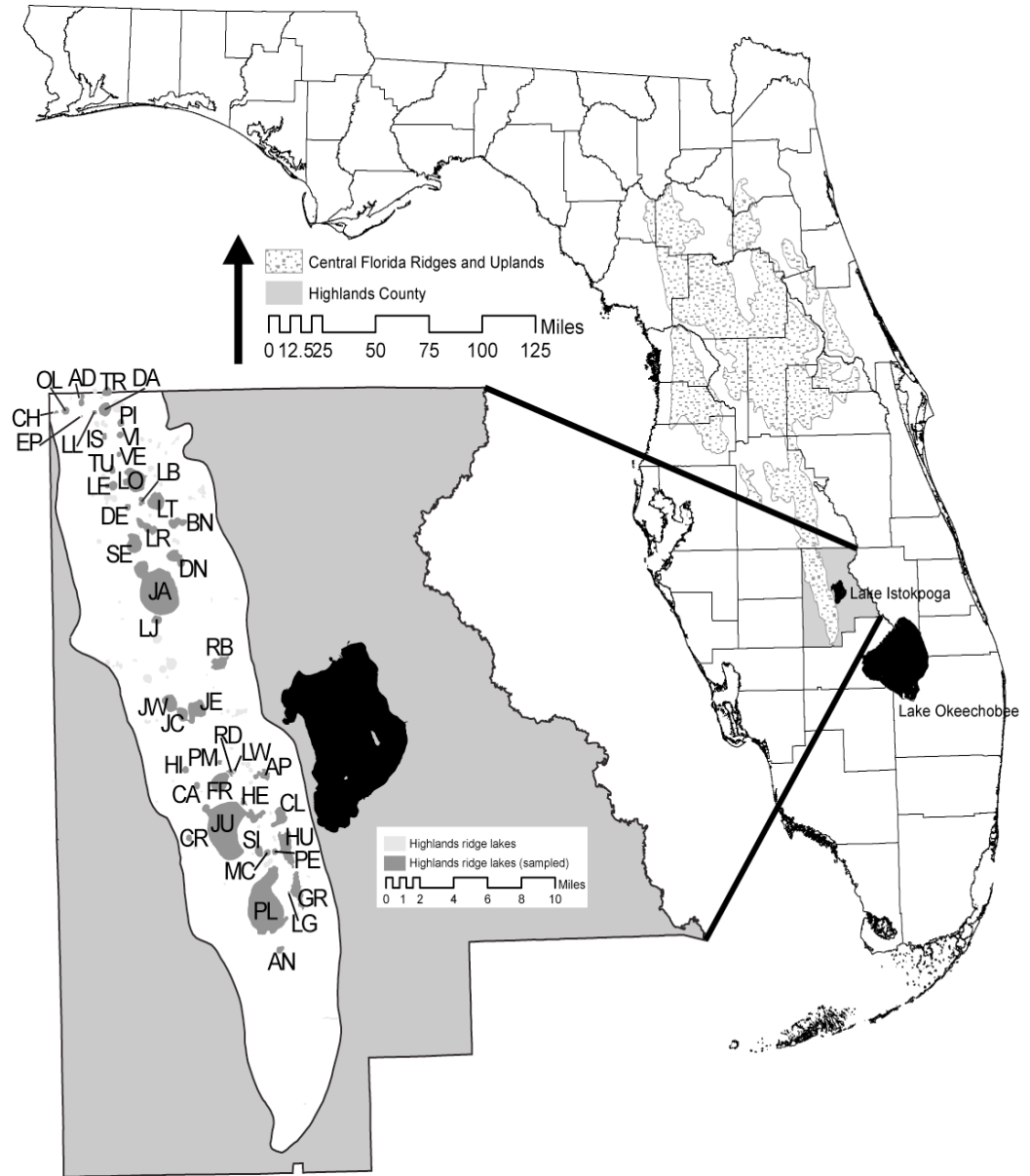


Figure 2: NMDS ordination of lakes based on diatom composition, labeled by habitat type (epiphytes (E), plankton (P), and sediment (S)).

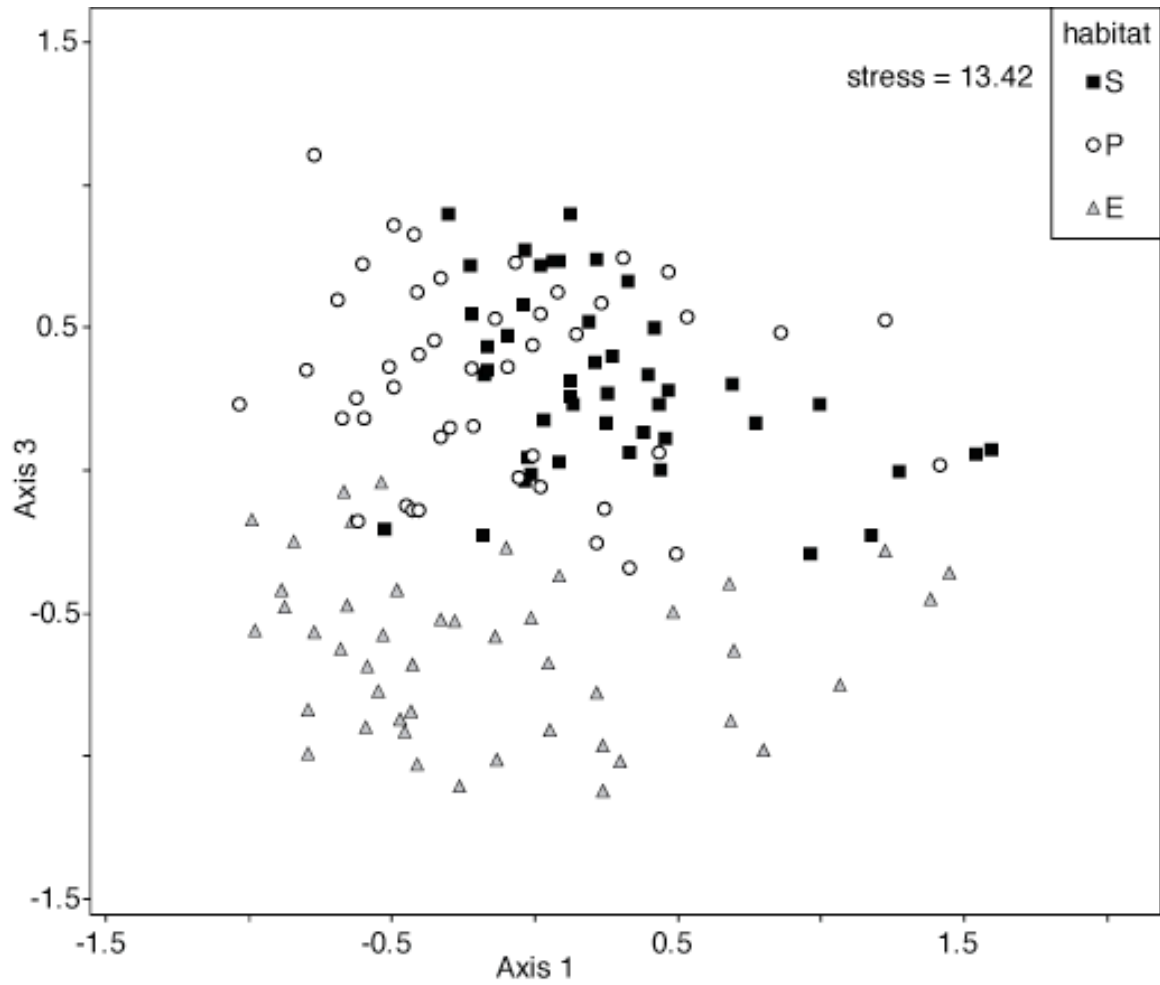


Figure 3: NMDS ordination biplot showing site scores of 46 lake epiphyte (a), plankton (b), and sediment (c) samples. Vectors represent environmental variables correlated with site scores (black arrows indicate $p < 0.01$, grey arrows indicate $0.01 < p < 0.05$).

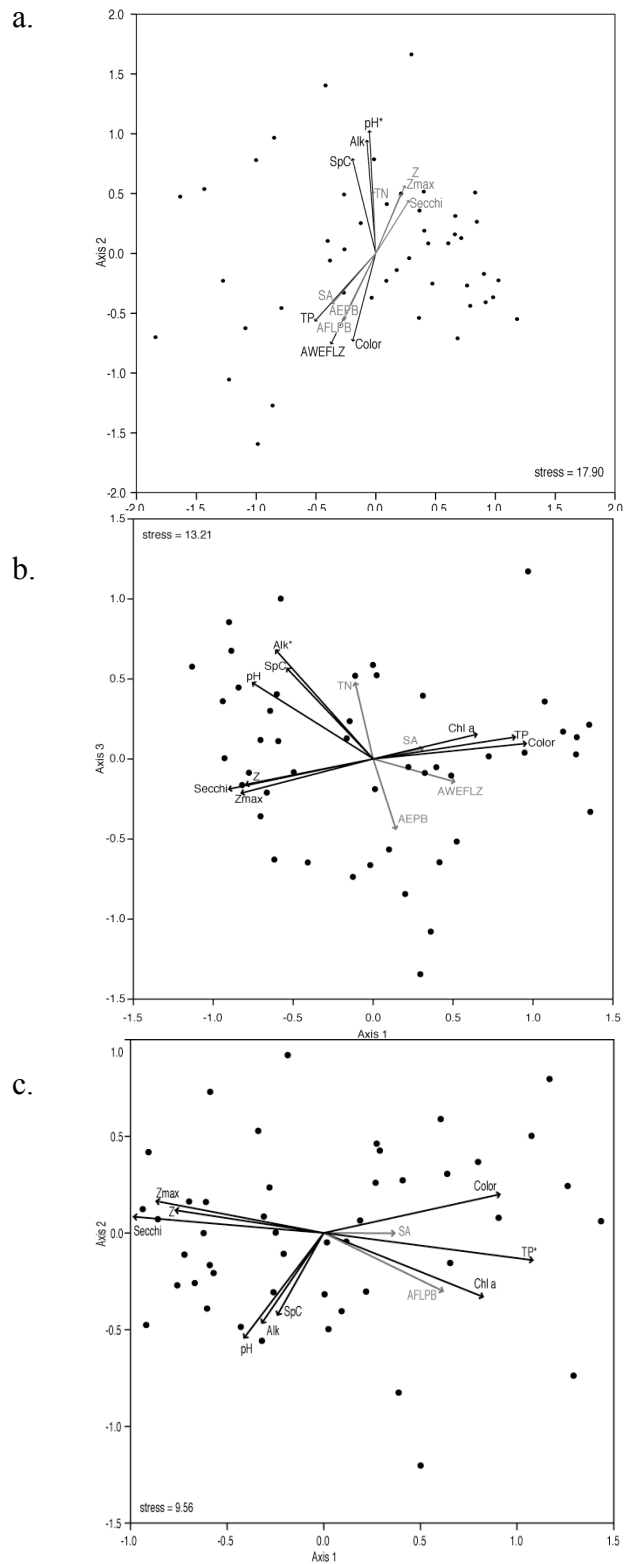
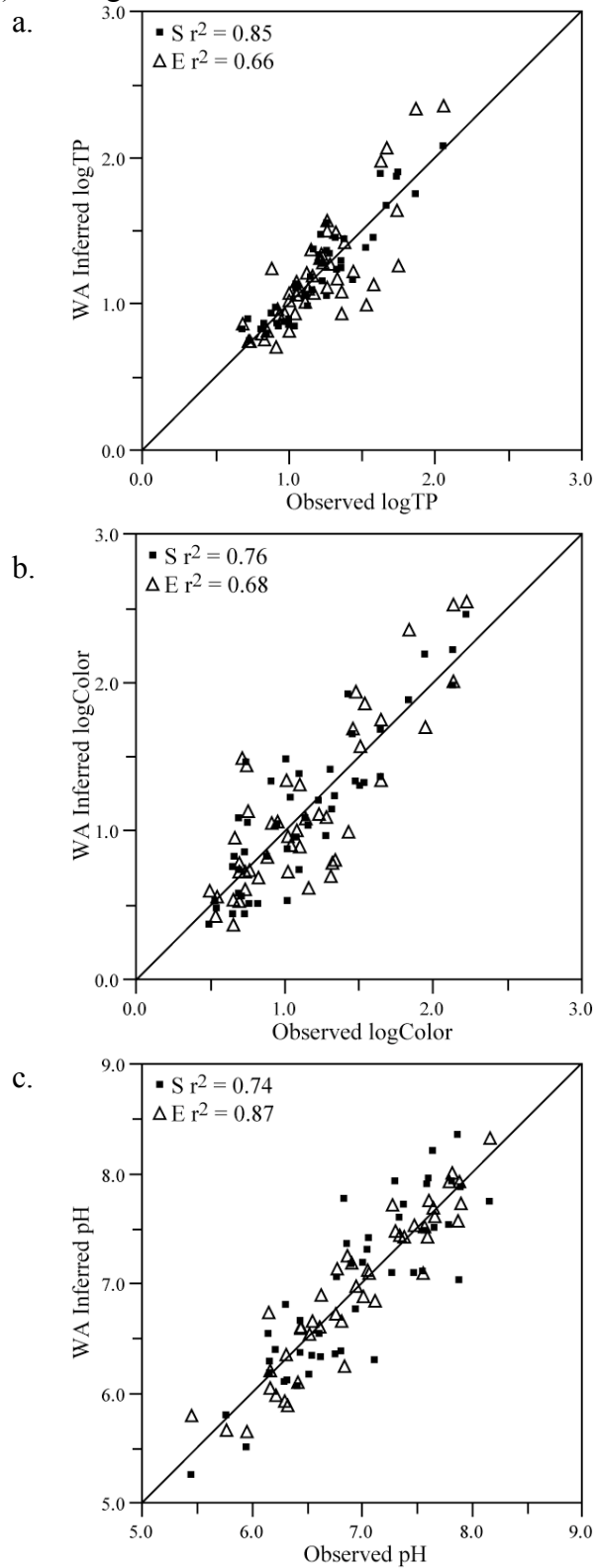


Figure 4: Plots of measured versus diatom-inferred TP (a), Color (b), and pH (c) for the sediment (S) and epiphyte (E) WA regression models with classical deshrinking.



3 DIATOM-BASED PALEOLIMNOLOGICAL RECONSTRUCTION OF LONG-TERM AND RECENT CLIMATE-DRIVEN AND ANTHROPOGENIC CHANGE FROM LAKE ANNIE, A DEEP SINKHOLE LAKE IN CENTRAL FLORIDA, U.S.A.

Abstract

Despite their sensitivity to climate change, few paleolimnological studies in Florida lakes have focused on changes in hydrology that are driven by climate change. Evidence from reconstructions of vegetation histories from sediment cores raise questions about the long-term hydrologic history of Florida lakes. A 25-year limnological dataset revealed recent climate-driven effects on Lake Annie. Using diatom microfossils, this research reconstructs both a long-term (11,000 year) record of hydrologic change and short-term (100 year) changes showing an interaction between hydrology and human effects on Lake Annie. Diatom-based weighted averaging (WA) models were used to reconstruct total Phosphorus (TP), color, and pH. The long-term record begins with Lake Annie as a wetland, then the lake filled to a high stand around 4000 years ago. A period of relative stability after that point was interrupted near the turn of the last century, with subtle changes in diatom communities suggesting acidification. An abrupt change is detected in the diatom communities around 1970 AD suggests the beginning of recovery from acidification, but concurrent hydrologic change intensified anthropogenic effects on the lake. Diatom evidence for alkalization and phosphorus loading correspond to changes seen in the limnological record from the lake.

Keywords: diatoms, sinkhole lake, Lake Wales Ridge, Lake Annie, color, total phosphorus, nutrients, pH, hydrology, paleolimnology

Introduction

The karst landscapes of Florida contains thousands of sinkhole lakes whose limnology is uniquely tied to the level of water table and regional precipitation (Brenner et al. 1990; Deevey 1988). Most Florida lake basins were dry at the beginning of the Holocene when sea levels and water tables were much lower than today. Only basins deep enough to maintain hydrologic connections held water before about 6000-8000 years ago (Brenner et al. 1990). Deeper lakes held water in the Pleistocene, and 50,000 years of vegetation history have been reconstructed (Grimm et al. 1993; Watts and Hansen 1994). It is not uncommon to find hiatuses in sedimentation after the beginning of the Holocene, even in deep Florida lakes (Watts et al. 1992; Watts and Stuiver 1980), raising questions about the hydrologic history of these lakes (Watts and Hansen 1994). Water table levels stabilized to modern levels between 5000-6000 years ago, as evidenced in sediment records across the Southeast by the expansion of wetland vegetation in pollen histories (Watts and Hansen 1988, 1994), the beginning of peat sedimentation in large freshwater wetlands (Gleason and Stone 1994; Scherer 1988), and the beginning of widespread sedimentation in shallow lake basins (Gaiser et al. 2001).

Despite suggestions of the great sensitivity to climate change in Florida lakes, little of the paleolimnological work in Florida has focused on hydrology. Florida lakes are also sensitive to changes caused by anthropogenic activities; and much of the paleolimnological research in Florida has focused on histories reconstructing the last 100 years. Inferences of pH and nutrient changes have been the primary applications of

diatoms in Florida sediments due to the strength of their association with these variables (Whitmore 1989). Consequently, Florida diatom assemblages have been used extensively to reconstruct anthropogenic pH (Sweets 1992) and nutrient (Brenner et al. 1999; Brenner et al. 1996; Deevey et al. 1986) changes. The intensity of change in these and other variables is susceptible to modification through changes in hydrology (Chapter 2), suggesting that diatoms could fill-in missing information about hydrologic change in Florida indirectly through their association with water chemistry variables. Diatoms can also respond directly to changes in hydrology, with shifts in diatom communities being especially evident with large fluctuations in water depth (Gaiser et al. 2001).

A 25 year limnological record from Lake Annie has revealed a recent shift in transparency related to hydrologic change (Gaiser et al. 2009), raising questions about the lakes susceptibility to change. This relatively deep lake is well known for its 37,000 year vegetation record from an 11 m sediment core showing sedimentation since the Pleistocene (Watts 1975). Samples from ^{14}C dated 11,000 year record and a more recent ^{210}Pb dated freeze core from the lake have been made available for diatom analysis.

The first objective of this research is to reconstruct the long-term history of Lake Annie, finding evidence from diatoms that shed light on the hydrologic change seen elsewhere in the Southeast, particularly stabilization of modern water levels in lakes and wetlands from the region 3-4000 years ago. The second objective is to reconstruct the short-term (~100 year) history of the lake for the purpose of refining the source of the recently observed changes seen in the lake (increased TP and pH, reduced transparency). It will also be interesting to note if any changes in the recent record might be related to

anthropogenic activity in what is considered to be a relatively pristine lake. Subtle alterations in human activity might amplify climate changes affecting the lake.

Study Area

Lake Annie (27°12'35" N latitude, -81°20'57" W longitude, 36.4 ha area) is a 20 m deep sinkhole lake on the property of Archbold Biological Station (ABS) near the town of Lake Placid in Highlands County, Florida (Figure 5). This deep lake has proven ideal for paleoecological study with an 11 m core revealing 37,000 years of vegetation history of the region (Watts 1975). Lake Annie is the southernmost in a string of sinkhole lakes on the Lake Wales Ridge (LWR), and is at the head of a watershed that runs north into Lake Placid and ultimately west to Lake Istokpoga and Lake Okeechobee. About 80% of the water delivered to the lake is through shallow groundwater with the remaining 20% supplied as rain (Battoe 1987). Two manmade ditches created in the 1940s deliver water to the lake intermittently from nearby seasonal wetlands (Battoe 1987; Layne 1979). Outflows include a natural surface stream connecting directly to Lake Placid (49%), seepage (38%), and evaporation (10%) (Sacks et al. 1998). The area around the lake is relatively undeveloped, with most of the lake's catchment area lying within the boundaries of ABS. Despite mostly pristine surroundings, the lake has recently seen a shift in color from clear to stained (Gaiser et al. In press).

Methods

In 1993 a 17.50 m piston core was recovered from the deepest part of the lake in 20.42 m of water, and 0.5 cc samples were removed for pollen analysis at 4 cm intervals (Grimm, unpublished data). Samples from the upper 15.54 m of the core that were not

used for pollen analysis were made available for diatom analysis. Diatoms were analyzed at 16-32 cm intervals at the top of the core, depending upon the quality of the microfossils in the samples. Preservation at the bottom of the core was poor; therefore analyses were attempted at wider intervals, between 24 and 126 cm. Additional core samples were inspected for macrofossils for radiocarbon dating, and 17 AMS radiocarbon dates were obtained from Lawrence Livermore National Laboratory Center for Accelerator Mass Spectrometry (CAMS) (species and dates presented in Table 9), the top 10 of which fall within the range of depths analyzed for diatoms. These dates were calibrated to calendar years using CALIB 4.2 software (Stuiver and Reimer 1993).

In order to characterize more recent changes in the lake, a 66 cm freeze core was recovered on May 30, 2007, near the location of the earlier piston coring. The upper 29 cm of this core was subsampled for diatoms at 1 cm intervals. Bulk sediment samples were sent to the St. Croix Watershed Research Station, MN for ^{210}Pb dating (Table 10). For each core separately, ages for samples without ^{14}C or ^{210}Pb dates were determined by linear interpolation between dates (Figure 6).

Each diatom sample was successively boiled in 30% H_2O_2 and 70% HNO_3 to remove organic material. The acidic water was decanted every 6 hours and the beaker refilled with distilled water until a neutral pH was achieved. Subsamples of cleaned material were dried onto 0.1-mm thick glass coverslips, which were permanently fixed with Naphrax[®] mounting medium onto glass slides. The number of diatom valves (including fragments) were counted in random, measured transects on one slide from each sample at 750x magnification on a Nikon E600 compound microscope. At least 500 diatom valves were identified to the species level using standard literature. Digital

photographs were recorded for each species using a Sony CCD camera fitted to the microscope (Chapter 4).

Data Analysis

The freeze core count data were combined with the piston core data for all initial numeric analyses after preliminary diatom examination revealed similarities between the bottom of the freeze core and the top of the piston core. In order to examine relationships of diatom composition among samples, I used cluster analyses. Stratigraphically constrained clustering by information content (CONIIC), with Orloci's chord distance as the distance measure, was used to delineate zones in the cores, using the program Psimpoll (Bennett 2008). To explore relationships between samples regardless of depth, relative Euclidean chord-distance measures were clustered using the unconstrained Ward's method implemented in PC-Ord (McCune and Mefford 1999). In order to discover individual diatom taxa indicative of different zones, indicator species analysis (Dufrêne and Legendre 1997) was performed on species with a maximum abundance of at least 5% in any sample using groups created in each of the clustering methods, with the number of groups chosen to maximize the number of significant indicators in each cluster.

Quantitative estimates of total phosphorus, color, and pH were made from core diatom assemblages using the calibration models created in Chapter 2. The discriminant function analysis created in Chapter 2 was used to predict habitat membership (epiphyte or plankton) of each core sample.

Results

Diatom stratigraphy

The sediments from both the freeze core and the piston core contained an abundance of intact diatoms. Only at the bottom of the piston core were problems encountered with preservation, where large and thinly silicified species were broken and usually unidentifiable, with identifiable valves sparsely encountered and obscured by increased levels of silt and sponge spicules. Species richness was higher in the freeze core than the long core (Figure 10).

The two cores were divided into 4 zones based on diatom species composition and CONIIC results. Zones 1 and 2 are comprised of all but one of the samples from the piston core (Figure 7) while zones 3 and 4 contain the freeze core, with zone 3 including a single sample from the piston core (Figure 8).

The oldest zone (1) covers a long time period from the base of counted samples (3596 cm) at nearly 11,000 years old to 4,000 years old (2967 cm). Eight species were found to be significant indicators of this zone. The most abundant diatom species throughout this zone is *Aulacoseira nygaardii*. *Fragilariforma spinulosa* peaks in abundance near the top of this zone, and is not present in the rest of the core. It may be appropriate to subdivide this zone into two sections, with the bottom three samples representing their own subzone. Poor preservation and an increase in sponge spicule total abundance were characteristic of this earliest section of zone 1.

Zone 2 represents the time period from 4,000 years ago to about 100 years ago, though the age boundary between zones 2 and 3 is unclear. The piston core was only analyzed for ^{14}C dates, and the diatom assemblage overlap between the two cores is not

100% at any point. *Eunotia carolina*, *Brachysira seriens*, and *Frustulia saxonica* are the most abundant species in zone 2, and they maintain this high abundance into zone 3. *Kobayasiella madumensis* becomes very abundant in zone 3, perhaps accounting for some of the differences between the two zones.

Zone 4 is defined by the rapid appearance of *Eunotia zasumenensis* and *Aulacoseira tenella*, two species known to be found together in the plankton of colored lakes (Eloranta 1986). The boundary between zones 3 and 4 falls between 11 and 12 cm in the freeze core, corresponding to a date of about 1970 A.D. Although the piston core was taken in 1993, these two abundant zone 4 species are completely absent from that core. Indicator species analysis revealed 26 significant indicators for zone 4, more than zones 2 (9 indicators) and 3 (14 indicators) combined.

When clustering was not restricted stratigraphically, samples from zone 2 clustered more closely with zone 4 than with either of its surrounding zones 1 and 3 (Figure 9). All but one zone 1 indicator is present in zone 3, and all zone 3 indicators are present in zone 1, with some attaining abundances near their zone 3 levels. Zone 3 indicator species *Frustrulia pseudomagaliesmontana* reaches its highest abundances in the transition between zones 1 and 2.

Calibration

Diatom assemblages from both cores had greater than 70% overlap with both epiphyte and sediment models (Figure 10). Diatom assemblages in the cores were represented by least 52% of species in either reference set, with an average overlap between core samples and either reference set of 72%. Overlap was consistently higher for the sediment set over the epiphyte set. The discriminant function analysis created in

Chapter 2 was applied to the core samples, and the majority of samples were predicted to be from an epiphytic habitat. Most of the samples predicted to be planktonic are from the upper 3 zones, especially in the freeze core. The level of epiphyte model overlap and the discriminant analysis results suggest that epiphytic species are delivered to the sediment from the littoral zone.

Both sediment and epiphyte models for TP, color, and pH were each applied to the two sediment cores (Figure 10). For each variable, weighted-averaging estimated optima of all taxa at each depth in the cores were combined to infer the level of the variable. Inferences of TP and pH were relatively consistent between epiphyte or sediment models. Color estimates, however, differed significantly between the two models. Estimate error values for all six models were lowest in the freeze core, perhaps due to the greater species richness in that core.

Total Phosphorus inferences from the epiphyte model were more variable and had higher error than inferences made from the sediment model. The sediment inferences showed stable low TP values throughout zones 1, 2, and 3, then an increase in zone 4. Epiphyte inferences peaked at some points during zones 1 and 2, but errors overlapped those of the lower inferences in those zones. The epiphyte model also inferred increased TP in zone 4.

The epiphyte and sediment models disagreed widely in their inferences of color, with estimates as much as 161 Pt-Co units apart. The average of the two inferences for the most recent core sample (55.4 Pt-Co units) is closer to actual modern measurements of color (44.4 Pt-Co units) than either the epiphyte (89.0 Pt-Co units) or sediment (21.7 Pt-Co units) inference.

Despite the fact that the sediment model was found to be stronger than the epiphyte model in cross-validation (Chapter 2), epiphyte inference errors were generally lower than sediment errors. All of the values estimated by the sediment model had overlapping errors, but some of the fluctuations estimated by the epiphyte model are significant. Peaks in color at 5500 years ago and around the transition between zones 1 and 2 correspond to peaks detected by the epiphyte TP model. Epiphyte inferred TP and color both peak in zone 3 around 60-65 years ago.

Inferred pH values from the epiphyte and sediment models are very similar, especially in zones 2, 3, and 4. Inferred pH values for both models show a gradual decrease in pH through zone 1, stability in zone 2, increasing again in the freeze core, especially in zone 4. Errors in inferred pH were much lower for the epiphyte model.

Discussion

Zone 1 (11,000-4,000 B.P.): A wetland becomes a lake

The abundance of sponge spicules and silt, coupled with the poor preservation of diatoms at the bottom of zone 1 suggest wetland conditions. Broken diatoms and excess silt are evidence of oxidized or reworked sediments subject to periodic drying. Sponges indicate attachment sites such as plant stems. The base of this record, at nearly 11,000 years old, corresponds to a peak in oak pollen associated with dry conditions in the region (Watts and Hansen 1994). The lake would have been at its minimum depth at this point. *Aulacoseira nygaardii* is the dominant diatom found at the bottom of zone 1. This taxon is known from slightly acidic waters with low TP (Siver et al. 2005) and is capable of colonizing an area quickly once hydrologic connections are available (Scherer 1988).

As sponge spicules and *A. nygaardii* decline, the acidophilic genera *Kobayasiella* and *Frustulia* rise in abundance, coincident with a decline in diatom inferred pH. A sudden peak in diatom inferred TP and color around 6,250 YBP coincides with spikes in abundance of tropical planktonic diatoms *Fragilariforma spinulosa* and *Aulacoseira herzogii*. *Aulacoseira herzogii*, a species tolerant of turbid conditions (Jewson et al. 1993), is probably the same species described in (Gaiser et al. 2001) as the dominant taxa during the first open water phase in Peat Bay, SC. The rise of *Asterionella ralfsii* v. *americana* accompanies another peak in diatom inferred TP and color at the end of zone 1. These lines of evidence support the idea of a great increase in depth during the last half of zone 1, perhaps accompanied by periods of rapid water delivery, which deliver excess nutrients and colored organic material to the lake.

Zone 2 (4,000-100 B.P.): Stable lake phase

The beginning of zone 2 at 4,000 YBP coincides with the estimated establishment of modern conditions across the Southeast United States 4,000-5,000 years ago. This time period is characterized by the stabilization of the composition of modern plant communities (Watts 1980) and lake levels (Gaiser et al. 2001), and the development of the Everglades (Davis et al. 1994). From 4,000 YBP, until the last 100 years, the Lake Annie diatom community changed very little. Diatom inferred pH and TP levels were stable, while diatom-inferred color stabilized in the middle of zone 2, declining steadily from a high level at the zone 1 to 2 transition.

Zone 3 (100-30 B.P.): Possible acidification

Most of the zone 3 indicators also found in (Siver et al. 2005) are described there as taxa present under very acidic conditions and the range of pH optima in (Camburn and Charles 2000) is 4.66-5.28 for the species present in their study. Furthermore, diatoms present both in the northeastern U.S. and Florida tend to have lower pH optima in Florida (Sweets et al. 1990). The reference set applied in this study (Chapter 2) only contains 2 lakes with a pH lower than the modern pH of Lake Annie (5.45 and 5.77 versus 5.95 for Annie). Diatom inferred pH throughout zones 2 and 3 is at the lowest level detectable by the reference set. Acid deposition has been shown to result in lowered pH in Florida lakes (Sweets 1992; Sweets et al. 1990) during the 20th century. Autecology of the zone 3 indicators, some of which are also present at the zone 1-2 transition, would suggest lower pH levels than those inferred. Some of the indicators that prefer low pH the most are indeed missing from the reference set. Reference set estimates of pH optima for some species are likely overestimates, with those diatoms having been collected in lakes with pH levels within the upper portion of their tolerance.

Color and TP inferred from epiphyte assemblages both show a zone peak at 1950 AD. It is interesting to note that this corresponds to a period of high rainfall and lake stage (Gaiser et al. 2009) that would result in greater delivery of nutrients and dissolved organic matter to the lake.

Zone 4 (1970 A.D. to present): Anthropogenic impacts and hydrologic change

Zone 4 is characterized by the rapid appearance of *Eunotia zasumenensis* and *Aulacoseira tenella*, two diatoms described from slightly acidic to neutral locations (Eloranta 1986; Siver et al. 2005). Their appearance, and the rapid decline of zone 2 and

3 indicators, coincides with an increase in diatom-inferred pH to levels not seen since zone 1. An increase in pH might be evidence of recovery from acidification, but human activities such as pumping of groundwater for irrigation has also been shown to result in alkalization of Florida lakes (Brenner et al. 2006). Recent increases in lake stage and rainfall will result in delivery of more water of a higher pH, regardless of the source. Increased connections to nearby humic wetlands could result in increased delivery of DOC to the lake, which has been shown to relate pH increase (Keller et al. 2005). Increased height of the water table also delivers more base cations present in the groundwater, increasing the acid neutralization capacity of the lake (Sweets et al. 1990). Though the source of the increased pH is likely climatic, increased delivery of humic water is enhanced by the manmade ditches dug during the early part of the 20th century. Flow of water through the ditches only occurred during big storm events in the past (Layne 1979), but now takes place more often, delivering water from wetlands and scrub forest located to the south of the lake (Gaiser et al. 2009).

A relatively large increase in diatom-inferred TP was estimated to take place during zone 4. The epiphyte model predicted a larger change than the sediment model, mostly due to the higher optima estimations for *Eunotia zasumenensis* and *Aulacoseira tenella* from the epiphyte model. Though the increase in sediment-inferred TP is less dramatic, the increase from the bottom to the top of the freeze core represents a doubling of estimated TP, which should not be considered trivial in an oligotrophic, P limited lake. Increased P delivery to the lake is likely coming from the same source as the increased color, namely increased water delivery from outside sources. The increased precipitation

and higher groundwater levels can only serve to exacerbate eutrophication no matter whether the source of nutrients is natural or anthropogenic.

Diatom inferred color trends differ between the sediment and epiphyte models, with epiphytes estimating a decrease in color during zone 4 while the sediments show an increase over the same period. Color estimates from either model are suspect due to their disparate interpretations of the diatom communities, but a distinct color signal was expected in zone 4. No diatom indicators of clear water conditions emerged anywhere in the recent record, despite the clarity observed in the lake during the 1970s and 1980s. The lake was probably stained throughout most of its history, and the relatively brief clear phase was not long enough to encourage the colonization of color-intolerant species.

Calibration model predictions

Epiphyte and sediment communities may be having very different reactions to color changes in the lake, or key indicators of color change could be missing from the reference sets. While epiphyte and sediment communities respond similarly to pH, TP and color appear to affect the two communities very differently. The difference in predictions could be due to lower species overlap with the epiphyte reference set. Differences in diversity and effective gradient of the environmental variable also has consequences for the accuracy of a calibration set (Denys 2007). While the levels of each variable might be more reliable for the sediment set, the exaggerations produced by the epiphyte set are still useful to examine because the experience of the gradient by diatom communities in an epiphytic habitat may be exaggerated as well.

Caution should be exercised when developing and applying calibration data to sediment cores. Interpreting inferences in a historical context is important, and the value of autecological species data cannot be underestimated.

Conclusions

The Lake Annie diatom record uncovers both a long-term and recent record of climatic change as well as evidence that anthropogenic activities may have exacerbated the impact of climate change on the lake. Infilling of the sinkhole with water to form a wetland resulted from sea level rise and consequent upsurge in the water table coupled with increased rainfall. Water levels and the lake's environment stabilized with climate around 4,000 years ago. The lake is now experiencing another round of increased hydrologic pressure in the context of anthropogenic climate change. Despite the seemingly pristine location, subtle human modifications to the lake and recent climate-driven hydrologic change have combined to shift the lake rapidly into a new paradigm after nearly 4,000 years of relative stability.

Acknowledgments

Financial support was provided in part by a Florida International University Dissertation Year Fellowship. E. Grimm supplied the piston core samples and ¹⁴C data that made this study possible. Thanks to P. Mueller for locating the piston core and facilitating additional sampling by A. C. Dieffenbacher-Krall, who expeditiously supplied missing samples for diatom analysis. W. Anderson provided equipment, expertise and assistance enabling the retrieval of the freeze core. I also appreciate the taxonomic and laboratory support provided by F. Tobias and A. Wachnicka.

Table 9: Accelerator mass spectrometer radiocarbon dates (^{14}C age in years before 1950) from the piston core analyzed by the Lawrence Livermore National Laboratory Center for Accelerator Mass Spectrometry (CAMS), standard deviation (1σ) of ages, calibrated age (in years before 1993) from CALIB 4.02 (Stuiver and Reimer 1993), in parentheses with 1σ age range, and material dated.

CAMS#	Depth (cm)	^{14}C age	1σ	Calibrated Age	Material dated
20879	2152 - 2156	500	60	649 (530) 337	pine needles
20880	2368 - 2376	1290	60	1297 (1211) 1066	charcoal
20881	2560 - 2564	1900	50	1947 (1840) 1713	pine needles
20882	2756 - 2760	2740	60	2955 (2840) 2749	charcoal
20883	2956 - 2960	3690	60	4226 (4026) 3842	charcoal
21766	3126 - 3134	4610	60	5571 (5331) 5050	charcoal
21767	3320 - 3328	5570	80	6538 (6361) 6196	charcoal
29111	3410 - 3414	6280	80	7416 (7187) 6952	acorn fragments
21768	3480 - 3488	8120	80	9398 (9079) 8723	charcoal
29112	3570 - 3574	9260	70	10636 (10428) 10239	acorn fragments
29113	3646 - 3650	9990	60	11901 (11431) 11228	acorn fragments
46208	3650 - 3654	10120	50	12255 (11706) 11341	acorn fragments
21769	3666 - 3670	10900	60	13136 (12954) 12655	wood
46209	3666 - 3670	10950	50	13149 (12983) 12665	Cyperaceae seeds
46210	3686 - 3690	11010	50	13169 (13017) 12671	Pistia stratiotes seeds
29114	3710 - 3714	10990	60	13165 (13005) 12665	Pistia stratiotes seeds
21770	3774 - 3778	11700	60	13983 (13613) 13444	wood

Table 10: Sediment accumulation and age in the freeze core, as determined by ^{210}Pb activity using the constant rate of supply model. Samples were analyzed by the St. Croix Watershed Research Station, MN.

Top of Interval (cm)	Base of Interval (cm)	Cum. Dry Mass (g/cm^2)	Unsup. Activity (pCi/g)	Error of Unsup. Act. ($\pm\text{s.d.}$)	Cum. Act. below Int. (pCi/cm^2)	Age: Base of Int. (yr)	Error of Age ($\pm\text{s.d.}$)	Date (A.D.)	Sediment Accum. ($\text{g}/\text{cm}^2 \text{ yr}$)	Error of Sed. Accum. ($\pm\text{s.d.}$)
0	2	0.1664	8.7472	0.3243	12.4924	3.54	0.69	2003.9	0.0470	0.00179
2	4	0.3328	8.4086	0.3713	11.0932	7.35	0.72	2000.1	0.0436	0.00194
4	6	0.5208	7.8813	0.2792	9.6115	11.96	0.76	1995.5	0.0408	0.00152
6	8	0.7308	6.8538	0.2711	8.1722	17.17	0.82	1990.2	0.0403	0.00166
8	10	0.9628	6.1223	0.2425	6.7518	23.30	0.90	1984.1	0.0378	0.00159
10	12	1.1948	4.6221	0.1995	5.6795	28.85	0.99	1978.6	0.0418	0.00196
12	14	1.4718	4.6911	0.1972	4.3801	37.20	1.15	1970.2	0.0332	0.00156
14	16	1.7038	4.3668	0.1710	3.3670	45.64	1.40	1961.8	0.0275	0.00137
16	18	1.9358	2.6327	0.1293	2.7562	52.07	1.64	1955.3	0.0361	0.00227
18	20	2.1678	2.2579	0.1171	2.2324	58.84	1.96	1948.6	0.0343	0.00243
22	24	2.6654	1.6404	0.1002	1.3448	75.12	2.53	1932.3	0.0293	0.00253
24	26	2.9198	1.3126	0.0886	1.0109	84.28	3.27	1923.1	0.0278	0.00293
26	28	3.1742	1.0253	0.0853	0.7501	93.86	4.28	1913.6	0.0265	0.00359
28	30	3.4286	0.7765	0.0697	0.5526	103.68	5.71	1903.7	0.0259	0.00443
30	32	3.6830	0.7814	0.0767	0.3538	117.99	8.72	1889.4	0.0178	0.00414
32	34	3.9374	0.6816	0.0734	0.1804	139.62	16.75	1867.8	0.0118	0.00457
36	38	4.4801	0.1289	0.0570	0.0434	185.38	42.80	1822.0	0.0144	0.01520

Figure 5: Map of Florida showing the location of Lake Annie in Highlands County (inset) in Florida.

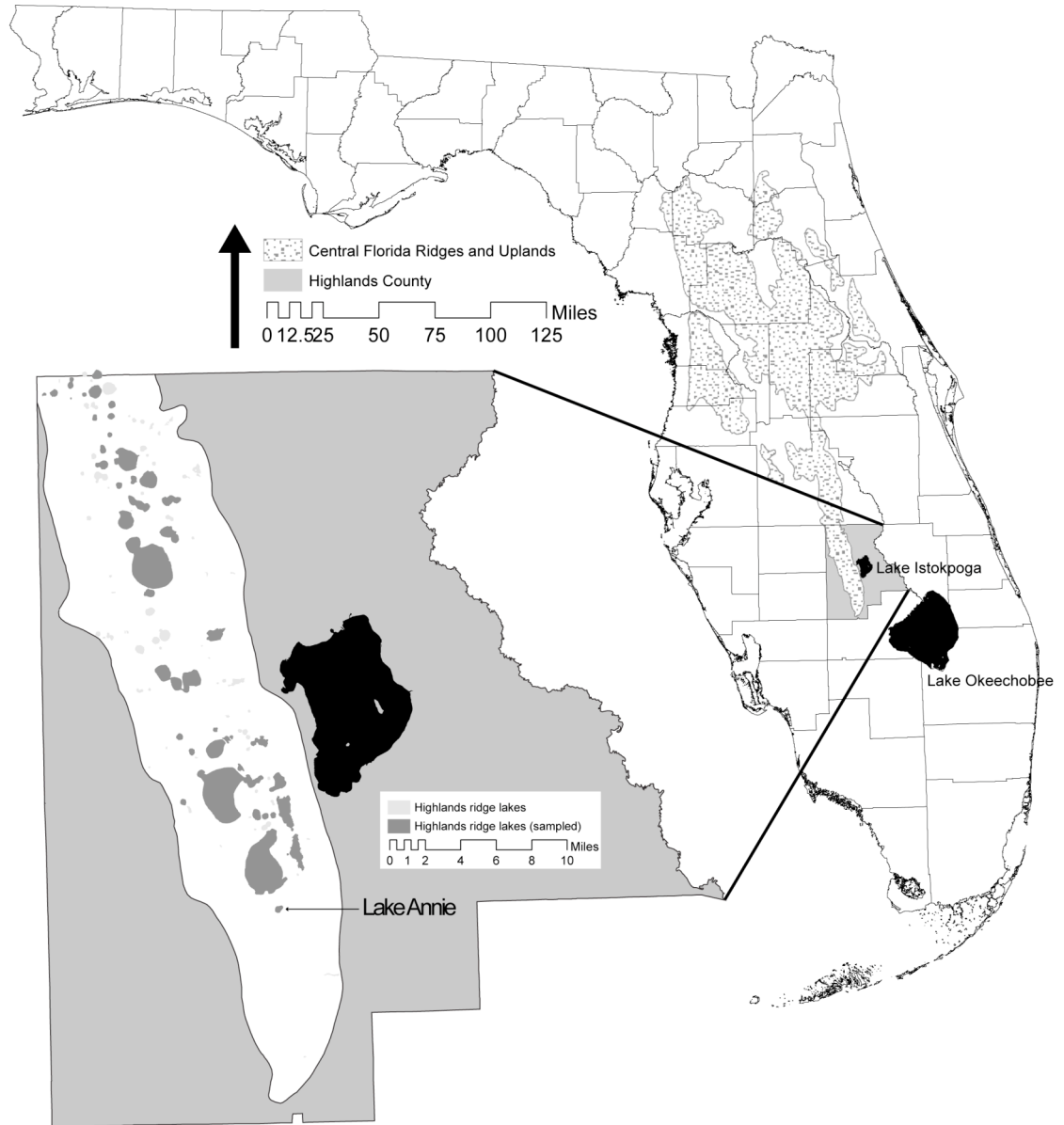


Figure 6: Age versus depth in (a) the piston core (circles = radiocarbon years before present, squares = calibrated ^{14}C dates) and (b) the freeze core (^{210}Pb age according to the constant rate of supply model).

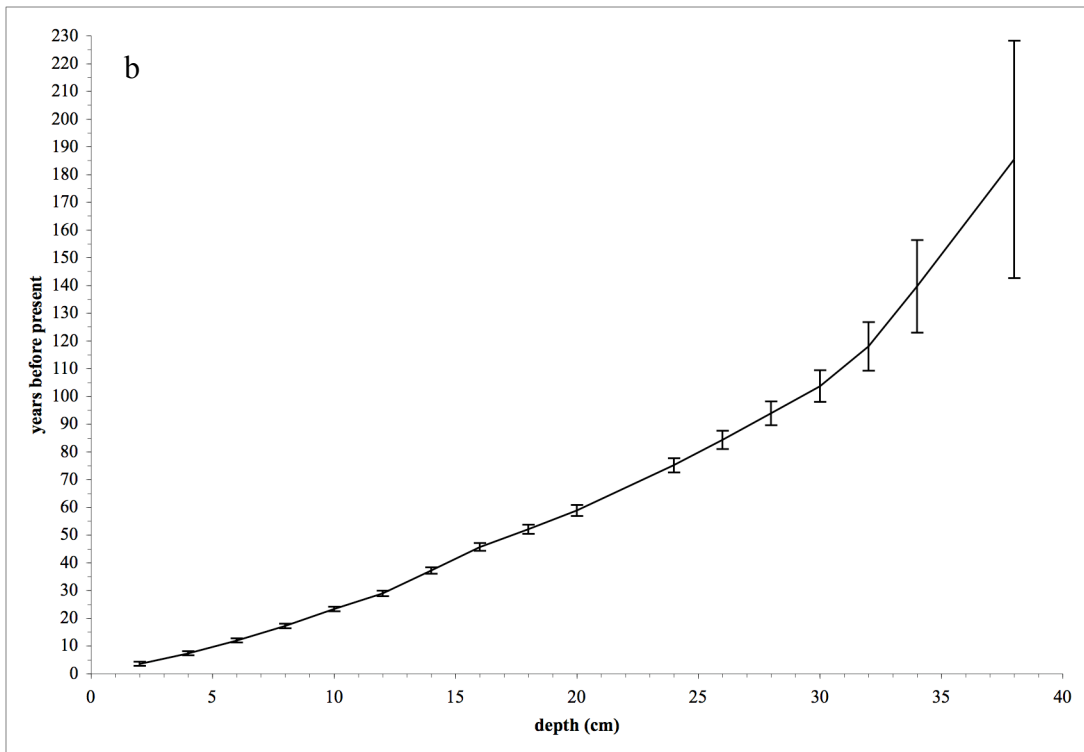
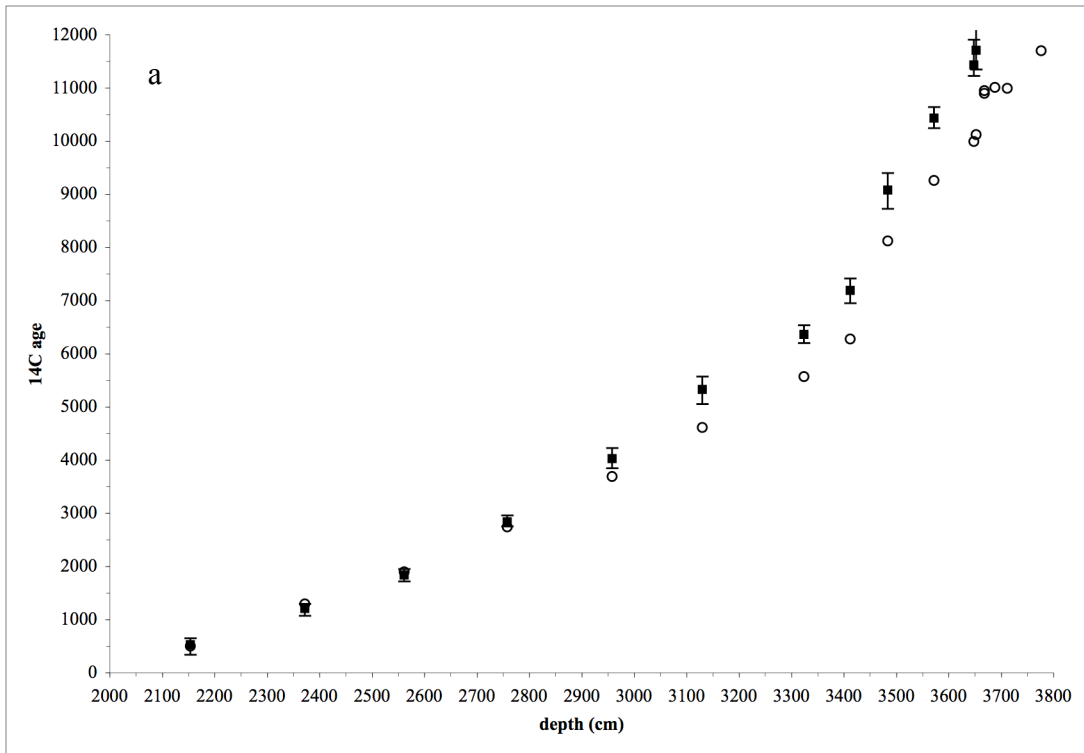


Figure 7: (3 pages) Stratigraphic diagram of both cores showing relative abundances of significant diatom indicators from zones delineated by CONIIC (dendrogram shown at end) and other abundant species (maximum relative abundance greater than 1%).

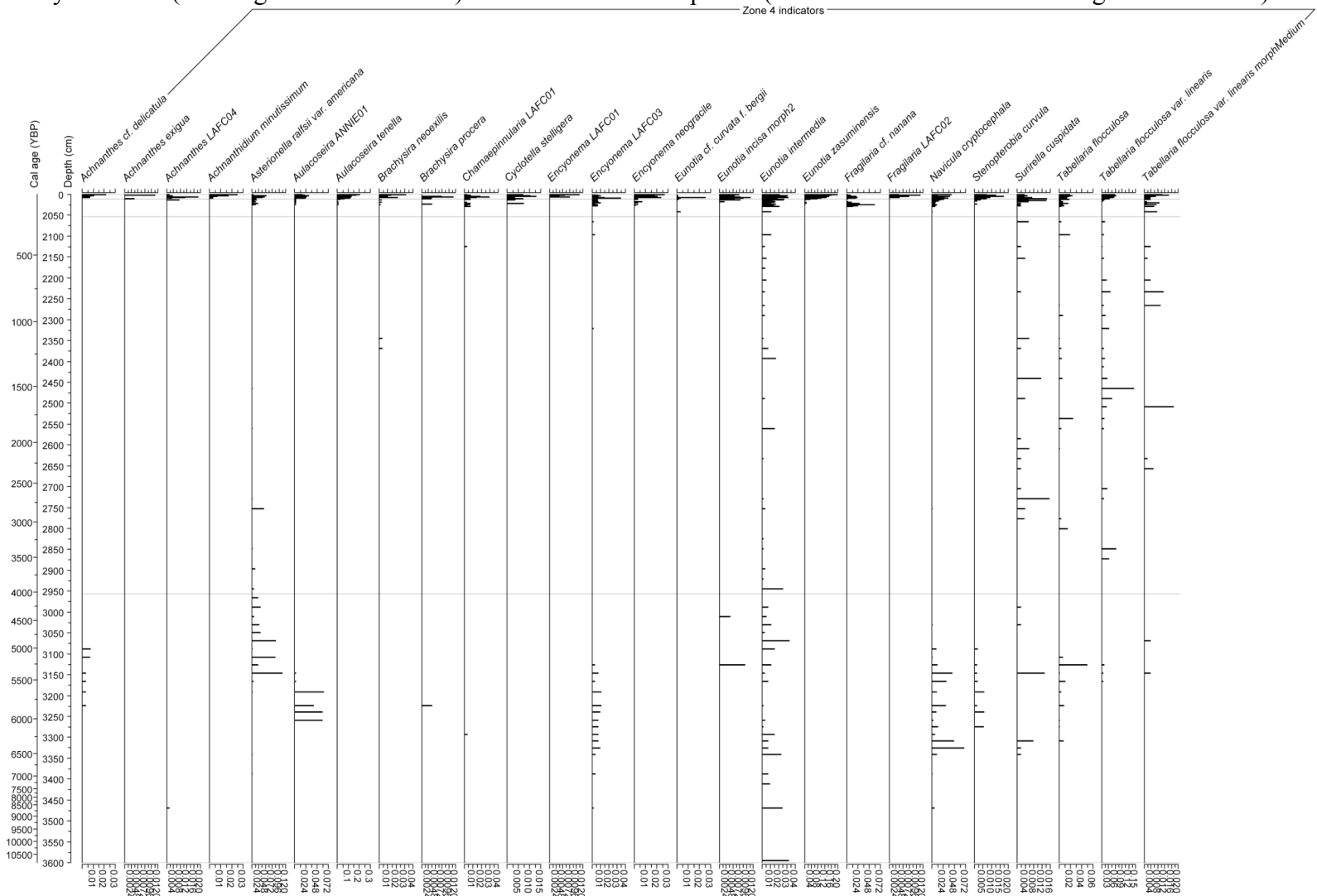


Figure 7 continued

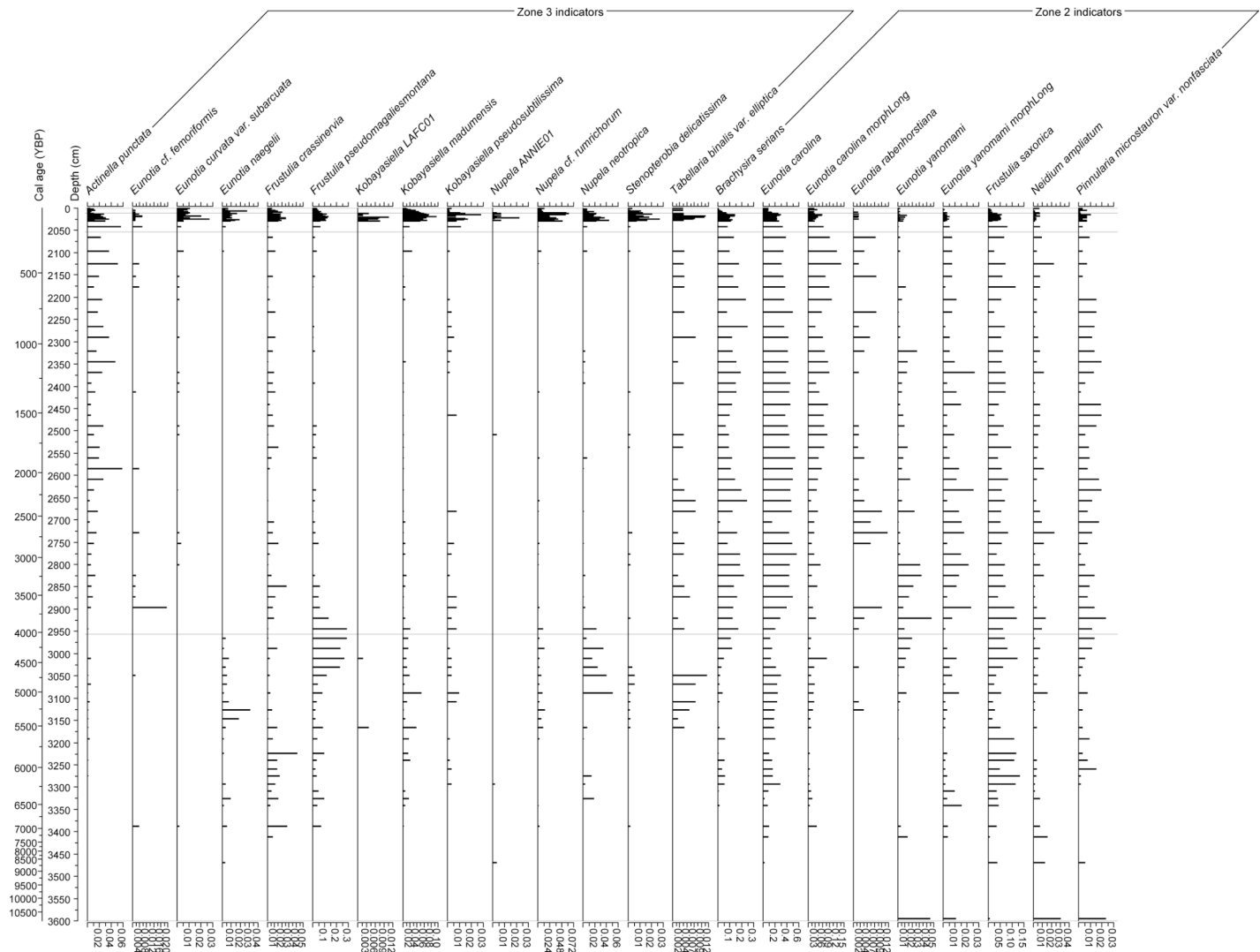


Figure 7 continued

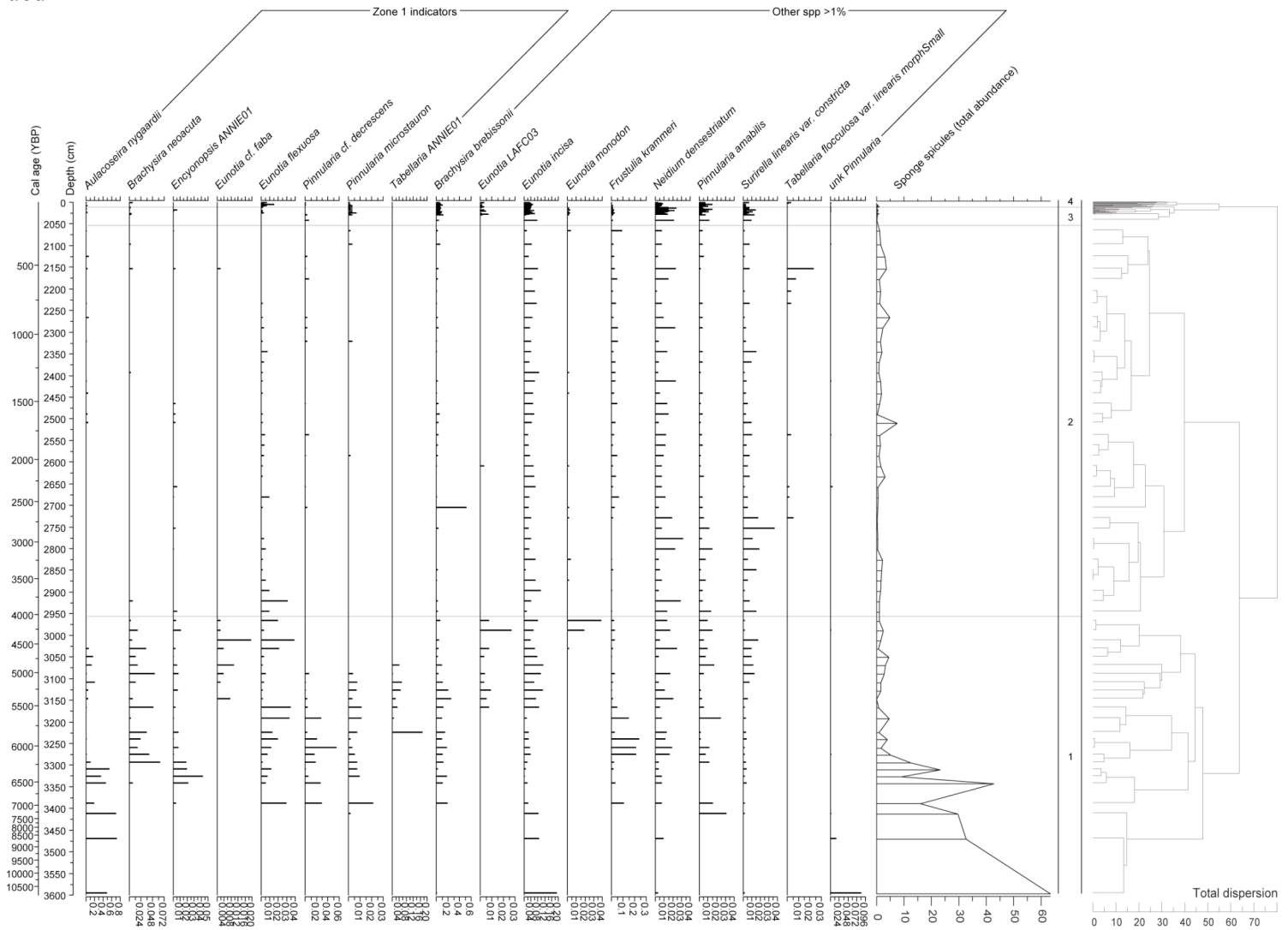


Figure 8: (3 pages) Stratigraphic diagram of freeze core and upper sample from piston core showing relative abundances of significant diatom indicators and other abundant species (maximum relative abundance greater than 1%). Only the two most recent zones (as determined by CONIIC dendrogram, shown at end) are presented.

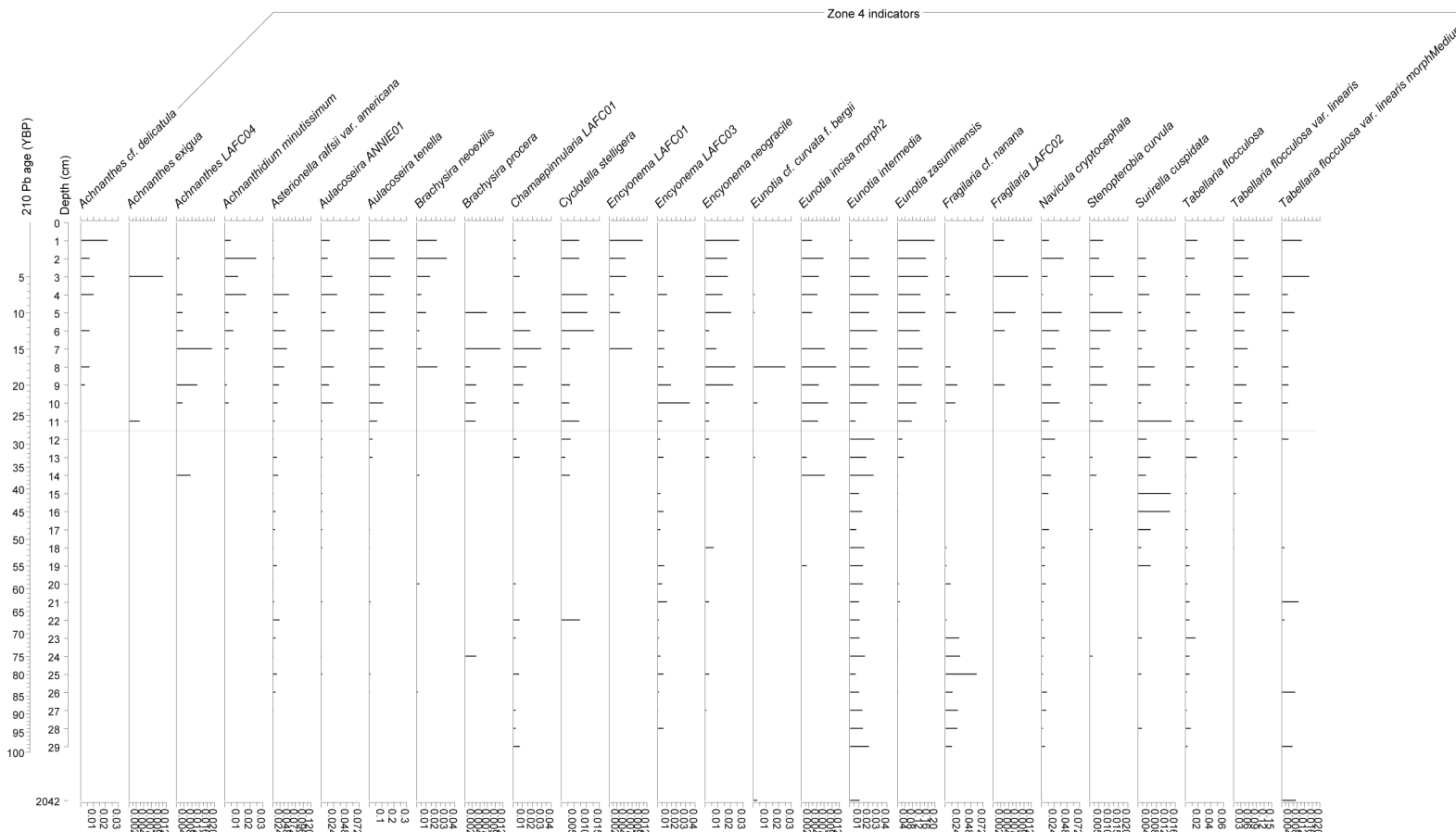


Figure 8 continued

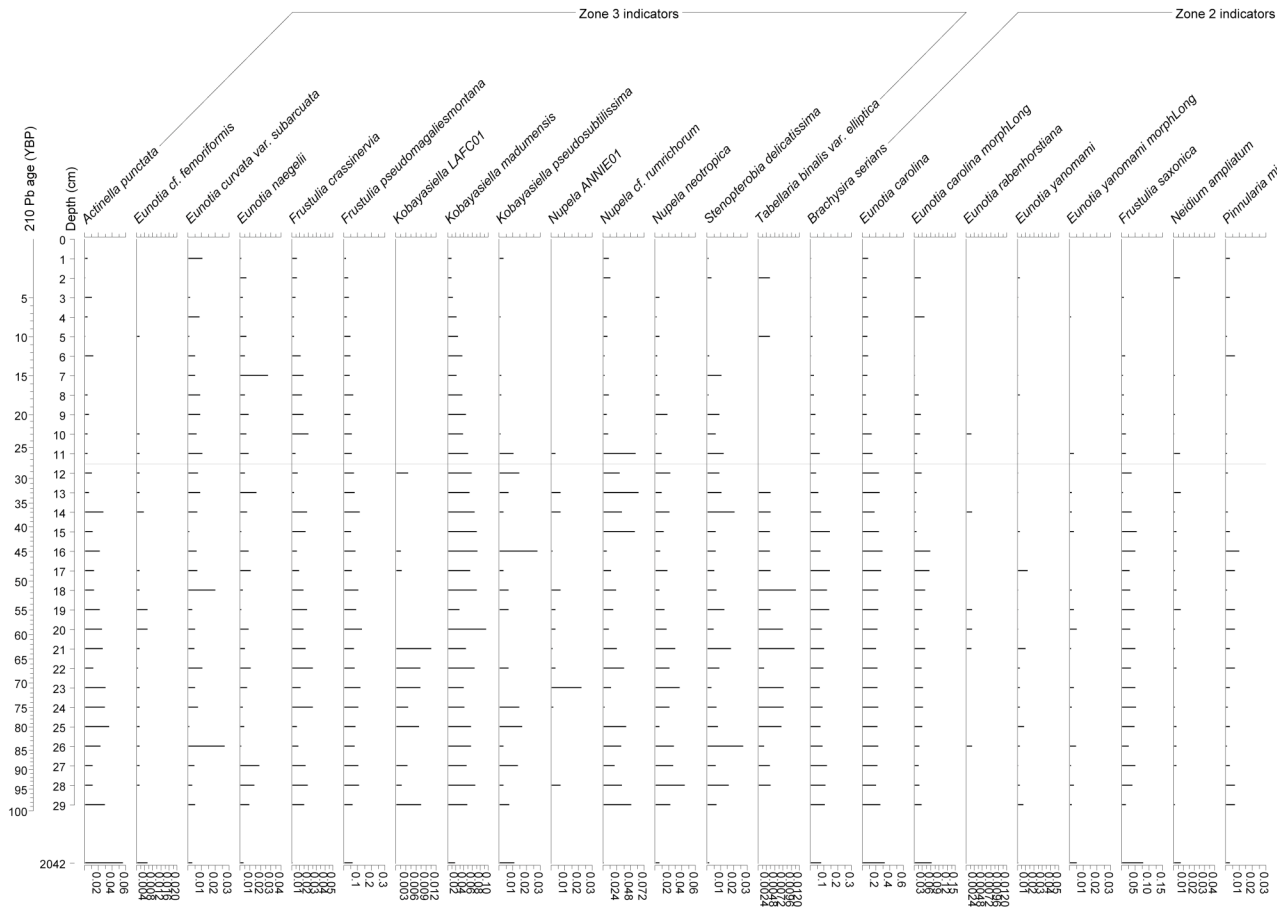


Figure 8 continued

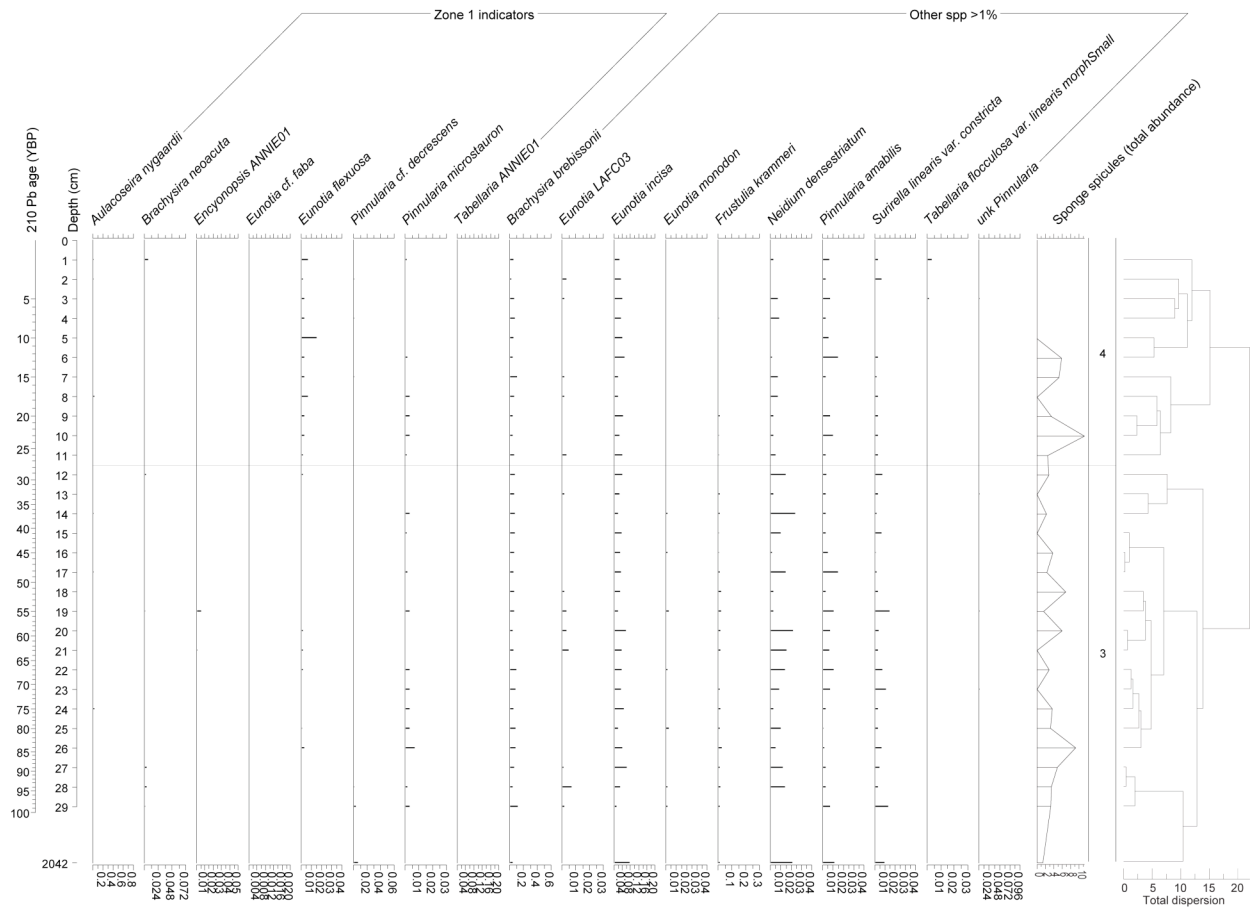


Figure 9: Unconstrained cluster dendrogram created by Ward's method using the relative Euclidean distance measure.

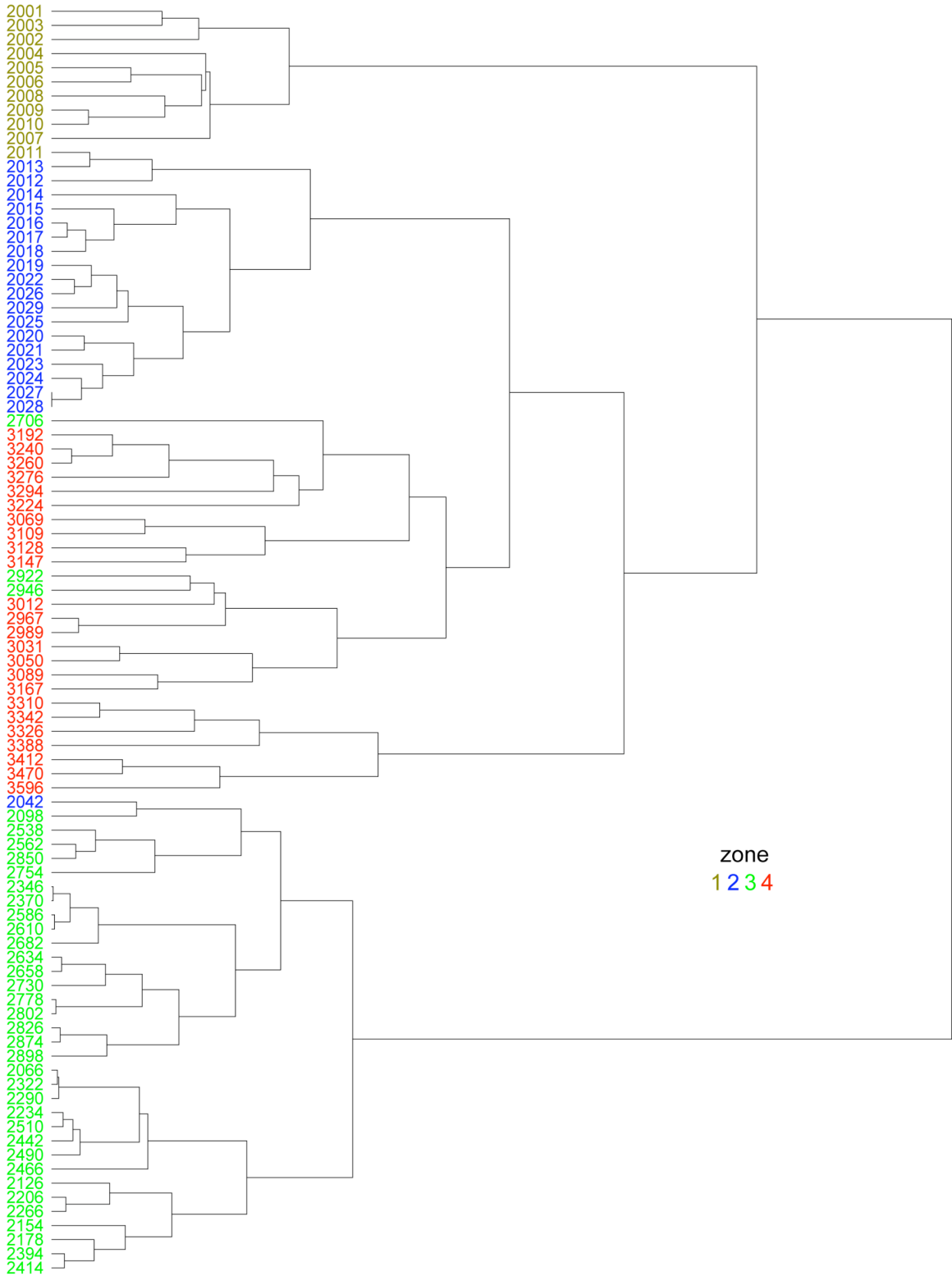
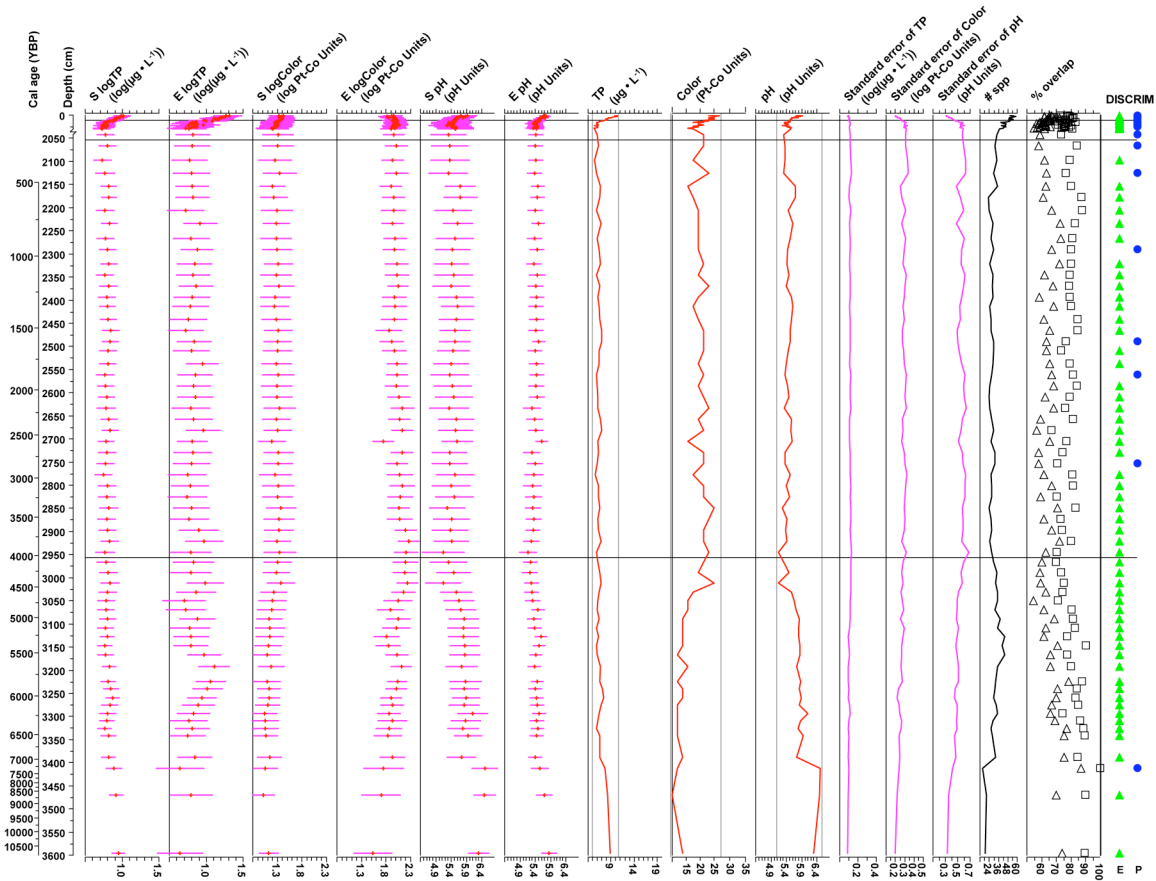


Figure 10: Diatom-based inferences of TP, color, and pH with associated standard errors from transfer functions produced in Chapter 2 are shown in the first 6 panels. Sediment results are graphed in the next 3 panels without error bars (TP and color are transformed back from log values), with grey lines representing minimum and maximum values for each variable. The next 3 panels illustrate the changes in standard error throughout the cores. Then there is one panel showing the number of species found at each depth in the core. The next to last panel shows the percentage of fossil taxa present in each of the modern diatom datasets (epiphyte = triangles, sediment = squares). The final panel displays the group (epiphyte = triangles, plankton = circles) predicted from the discriminant analysis for each depth.



4 FRESHWATER DIATOMS FROM HIGHLANDS COUNTY FLORIDA, U.S.A.

Introduction

While diatoms have been used extensively as indicators and for paleolimnological reconstructions in Florida lakes, a photographed diatom flora from South Central Florida lakes has not been published. The best available checklist of Florida lake diatoms from the area, which includes their pH and trophic state preferences, is that from Whitmore (1989), however nomenclatural changes and the lack of photographs make comparisons to other studies difficult. The nearest photographed flora available from Florida is from the Paleocological Investigation of Recent Lake Acidification (PIRLA) project in northern Florida (Camburn et al. 1986), t

Diatoms reviewed in this survey were identified in order to develop models predicting total phosphorus, pH, and color (Chapter 2) for paleolimnological reconstruction (Chapter 3). Photographs provided from this research will serve to enhance the capacity for future comparison to other diatom research in Florida. The objective of this study is to characterize the diatom flora from Highlands County with photographs and references to similar taxa in the literature.

Materials and Methods

Study area

The 46 solution lakes sampled for this study are located along the Lake Wales Ridge (LWR), the southernmost portion of the Central Florida ridges and uplands ecoregion (Griffith et al. Undated). The LWR is a 200-mile long line of relict coastal

beach sands overlying limestone bedrock, peppered by hundreds of lakes formed by karst processes (White 1970). All of the study lakes are located in Highlands County, on the southernmost portion of the LWR (Figure 1). Candidate lakes were chosen from those with water chemistry data available from the volunteer lake monitoring program, Florida LAKEWATCH (LAKEWATCH 2004). Emphasis was placed upon finding lakes with a wide range of color and maximum depth.

The climate of Highlands County is humid and subtropical. Seasonal variation is characterized by a warm wet season from June to September and a cool dry season from October to May. Rainfall averages 126 cm per year, with about 60% of that falling during the summer. The vegetation of the area is dominated by Florida scrub habitat, growing on acidic, sandy soils, however no more than 20% of the original extent of this habitat remains, the rest having been developed for citrus agriculture and residences (Christman and Judd 1990). A few of the lakes sampled for this study were located in an area with more or less pristine surroundings, but most were impacted in some way by development.

Collection of samples

Modern diatom samples were collected from all lakes during a two-week period in September 2003. At the deepest point in each lake, sediment samples were collected from the sediment-water interface using an Ekman dredge, and approximately the top 1cm of sediment was saved for analysis. On the same day, living diatoms were qualitatively sampled from each lake. Plankton was collected in each lake using a 20- μm mesh plankton net, and a periphyton or epiphyton sample was collected from the littoral

zone of each lake, taking care to sample proportionately from the different epiphytic habitats representative of each lake.

A ^{14}C dated 11,000 year record and a more recent ^{210}Pb dated freeze core from Lake Annie were also sampled for diatoms. In 1993 a 17.50 m piston core was recovered from the deepest part of the lake in 20.42 m of water, and 0.5 cc samples were removed for pollen analysis at 4 cm intervals (Grimm, unpublished data). Samples from the upper 15.54 m of the core that were not used for pollen analysis were made available for diatom analysis. Diatoms were analyzed at 16-32 cm intervals at the top of the core, depending upon the quality of the microfossils in the samples. Preservation at the bottom of the core was poor; therefore analyses were attempted at wider intervals, between 24 and 126 cm. In order to characterize more recent changes in the lake, a 66 cm freeze core was recovered on May 30, 2007, near the location of the earlier piston coring. The upper 29 cm of this core was subsampled for diatoms at 1 cm intervals.

Sample processing and counting

Organic material was removed from each sample by successively boiling in 30% H_2O_2 and 70% HNO_3 . After allowing the diatoms to settle, the acidic water was repeatedly decanted and the beaker refilled with distilled water until a neutral pH was achieved. Subsamples of cleaned material were dried onto 0.1-mm thick glass coverslips, which were permanently fixed with Naphrax® mounting medium onto glass slides. The number of diatom valves (including fragments) were counted in random, measured transects on one slide from each sample at 750x magnification on a Nikon E600 compound microscope. At least 500 diatom valves were identified to the species level using standard literature (Camburn and Charles 2000; Krammer 1997a, b, 2000, 2002;

Lange-Bertalot 1993; Lange-Bertalot and Moser 1994; Metzeltin and Lange-Bertalot 1998, 2007; Reichardt 1999; Siver et al. 2005) and taxonomic articles (Ludwig et al. 2008; Tobias and Gaiser 2006). Digital photographs were recorded for each species using a Sony CCD camera fitted to the microscope.

Water chemistry data

The primary source of environmental data was Florida LAKEWATCH, a program using trained volunteers to collect samples that are later analyzed by professionals (LAKEWATCH 2004). This strategy allows for more frequent monitoring and the inclusion of far more water bodies than could ordinarily be examined, while maintaining a high level of data quality (Canfield et al. 2002). Data from the Southwest Florida Water Management District (unpublished data) and the United States Geological Survey (USGS 2008) was averaged with the LW data when available. Details of the methods used to perform chemical analyses of samples can be found in (LAKEWATCH 2004).

Total Phosphorous (TP) and Color values were averaged as follows: Replicates sampled on the same day were averaged, and then these daily averages were averaged with any other daily averages from the same month. Quarterly averages were computed by averaging the monthly averages available in three-month groups (January-March, April-June, July-September, October-December). For those years that had at least 2 quarterly averages available, yearly averages were computed. Yearly averages from the years between 2000 and 2003 were used to calculate the lake average. Measurements of pH were taken at less regular intervals, therefore lake averages for these data represent averages of measurements taken on 1 to 4 different days between 1995 and 2003.

Results and Discussion

Environmental variation

Although the 46 sampled lakes reside very close together and are situated on similar substrates, they varied greatly in depth, surface area, and water chemistry (Tables 1 and 2). The ranges of values for TP (4.9-114.9 $\mu\text{g/L}$) and color (3.1-168.8 Pt-Co units) were large, but most values occurred at the lower end of these gradients (averaging 21.3 $\mu\text{g/L}$ and 25.6 Pt-Co units, respectively). The range of pH values (5.45-8.16) included both acidic and alkaline sites, with an average (6.94) near neutral.

Diatom distribution

I identified 310 taxa from approximately 56 genera from plankton, epiphytes, and recent sediments in the 46 survey lakes. Additional fossil diatoms from the paleo-sediments of Lake Annie are also included in this count.

Comparative studies

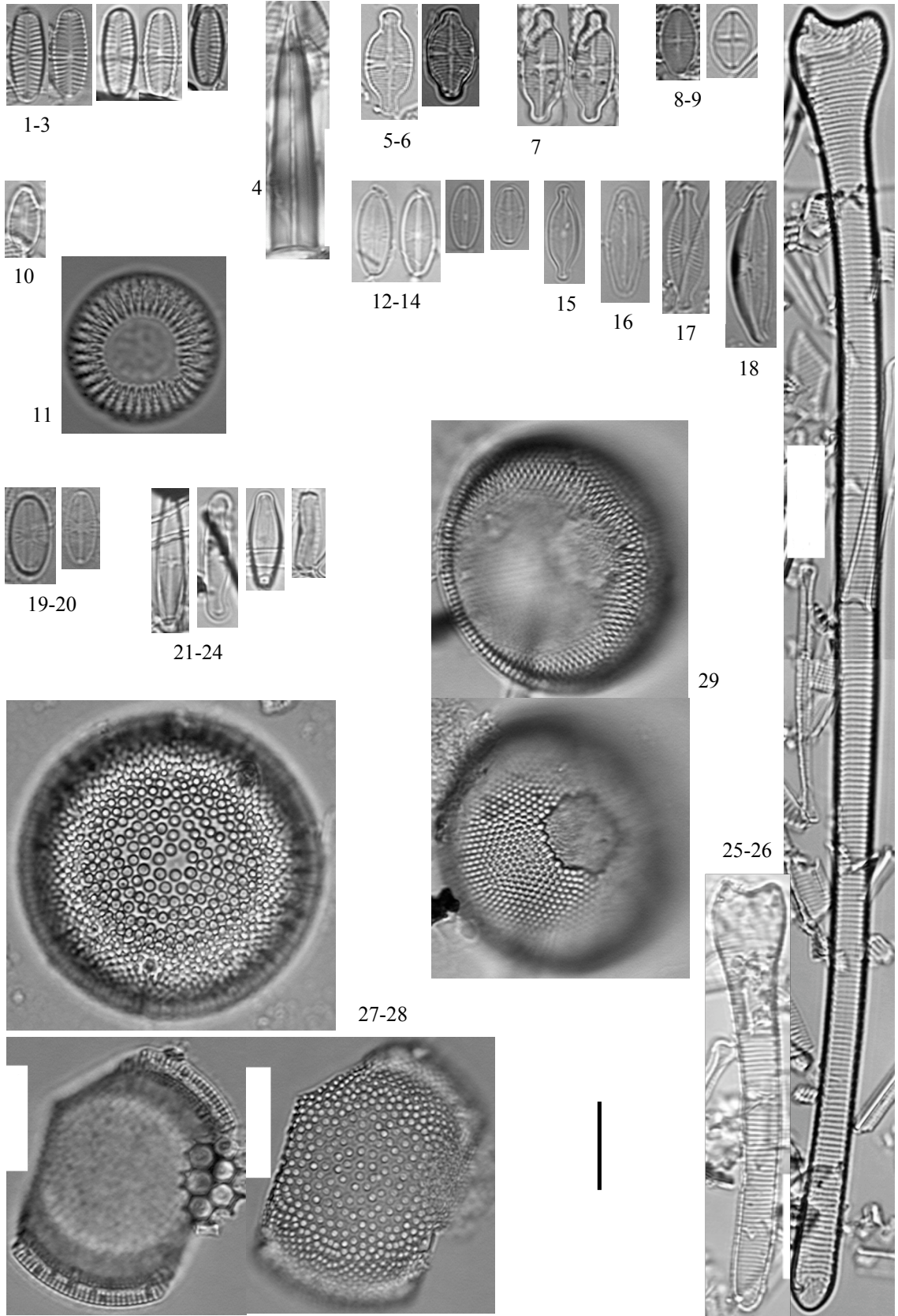
The flora of Highlands County is similar to that of Whitmore (1989), though nomenclatural changes and the lack of photographs make comparisons difficult. Highlands County diatom assemblages also resemble those found from the Paleocological Investigation of Recent Lake Acidification (PIRLA) project in northern Florida (Camburn et al. 1986), though those lakes averaged 0.50 pH units lower than the Highlands County lakes (Sweets et al. 1990). The flora overlaps with floras found throughout the Eastern United States, including those from South Carolina (Gaiser and Johansen 2000), New York (Camburn and Charles 2000), and Massachusetts (Siver et al.

2005). A number of diatoms from tropical floras are also found in Highlands County (Metzeltin and Lange-Bertalot 1998, 2007).

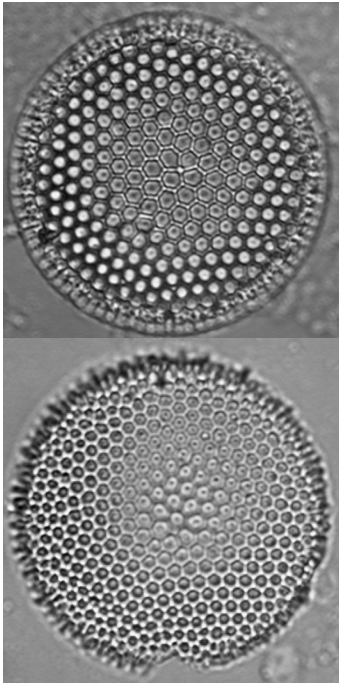
Annotated list of the diatoms

Diatom taxa are listed on the following pages in alphabetical order, accompanied (where appropriate) by literature references.

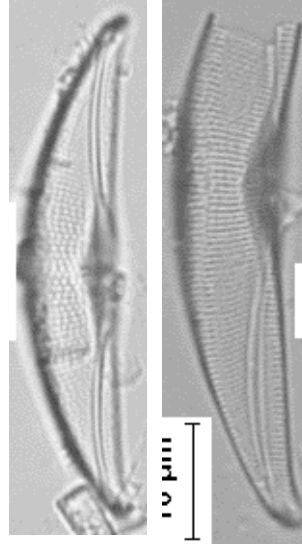
- Pl. 1-3 *Achnanthes delicatula* (Kützing) Brun 1880
- Pl. 4 Sponge spicule
- Pl. 5-7 *Achnanthes exigua* Grunow in Cleve & Grunow 1880
- Pl. 8-9 *Achnanthes exigua* var. *elliptica* Hustedt 1937
- Pl. 10 *Achnanthes* sp. 1
- Pl. 11 *Cyclostephanos* cf. *dubius* (Fricke) Round 1982
- Pl. 12-14 *Achnanthes* sp. 2
- Pl. 15 *Achnanthes* sp. 3
- Pl. 16 *Achnanthes* sp. 4
- Pl. 17 *Achnanthes* sp. 5
- Pl. 18 *Achnanthidium* sp. 1
- Pl. 19-20 *Achnanthidium* sp. 2
- Pl. 21-24 *Achnanthidium minutissimum* (Kützing) Czarnecki 1994
(Siver et al. 2005; Camburn and Charles 2000)
- Pl. 25-26 *Actinella punctata* Lewis 1864
(Metzeltin and Lange-Bertalot 2007; Camburn and Charles 2000)
- Pl. 27-28 *Actinocyclus* sp. 1
- Pl. 29 *Actinocyclus* sp. 2



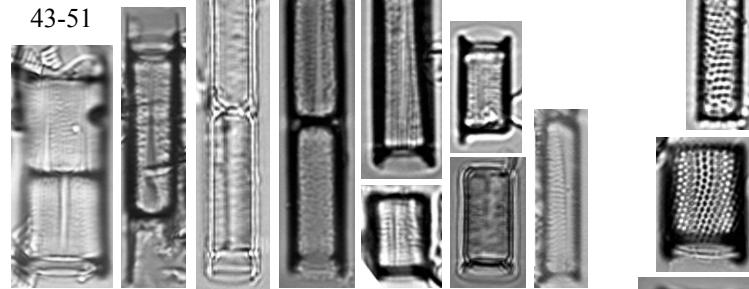
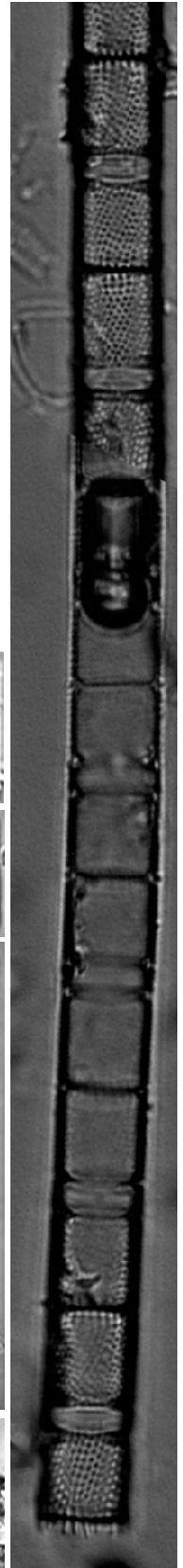
- Pl. 30 *Actinocyclus* sp. 3
- Pl. 31-32 *Amphora sulcata* Brébisson 1854
- Pl. 33-34 *Amphora ovalis* (Kützing) Kützing 1844
(Siver et al. 2005; Camburn and Charles 2000)
- Pl. 35 *Asterionella ralfsii* var. *americana* Körner 1970
(Siver et al. 2005; Camburn and Charles 2000)
- Pl. 36-42 *Aulacoseira ambigua* (Grunow) Simonsen 1979
(Metzeltin and Lange-Bertalot 2007)
- Pl. 43-51 *Aulacoseira herzogii* (Lemmermann) Simonsen 1979
(Metzeltin and Lange-Bertalot 2007)
- Pl. 52 *Aulacoseira* sp. 1
- Pl. 53 *Aulacoseira* cf. *perglabra* (Østrup) Haworth 1990
(Siver et al. 2005; Camburn and Charles 2000)



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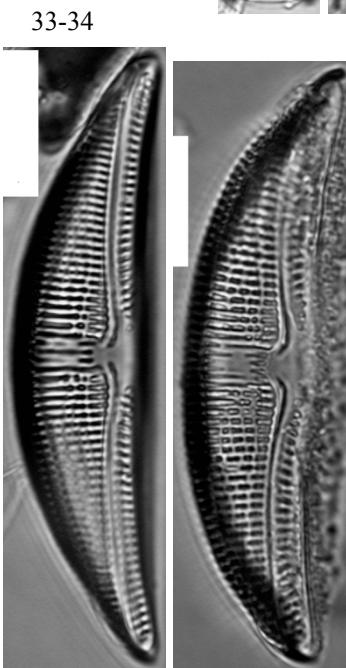


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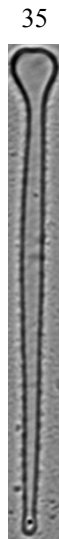


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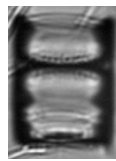
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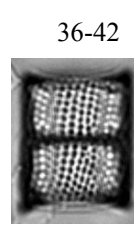
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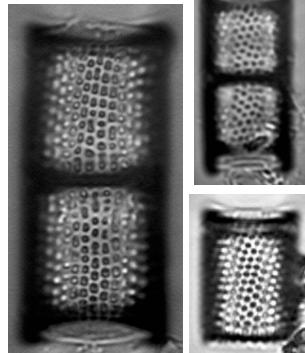
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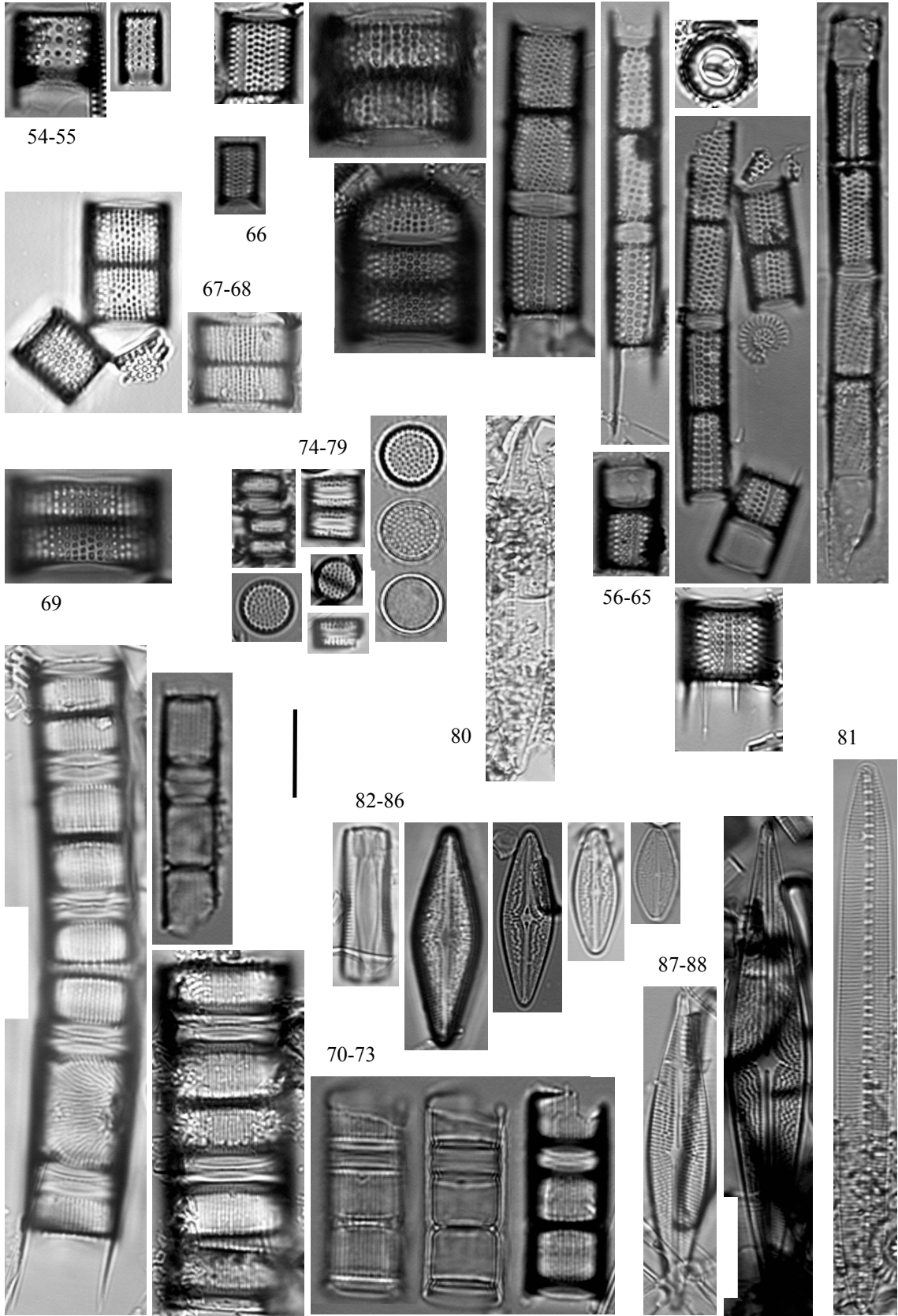
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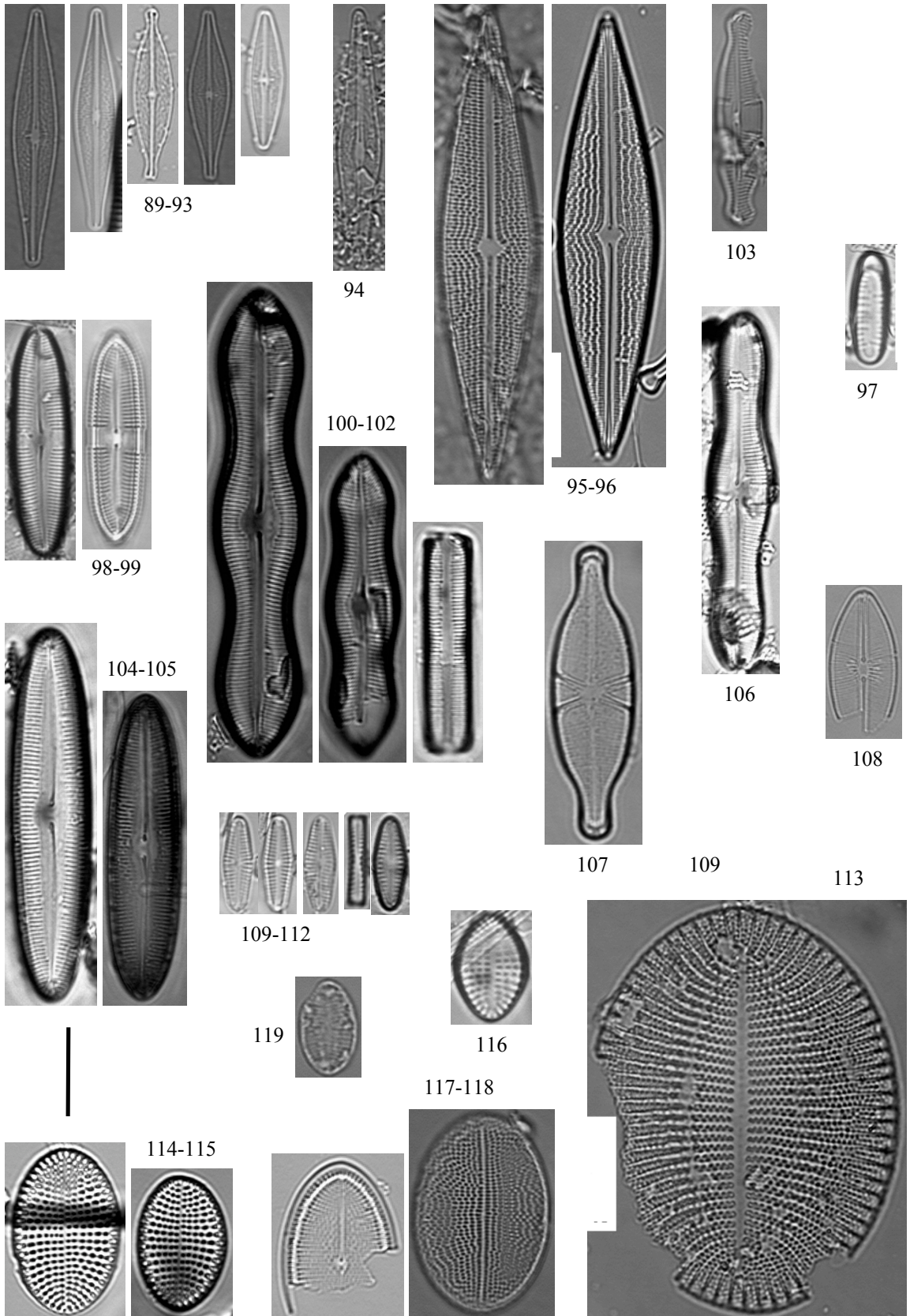
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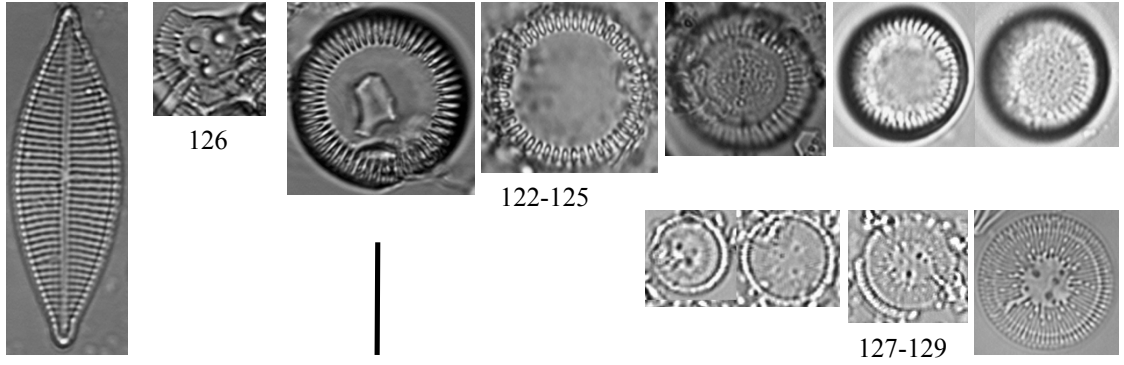
- Pl. 54-55 *Aulacoseira crassipunctata* K. Krammer 1991
(Siver et al. 2005)
- Pl. 56-65 *Aulacoseira granulata* (Ehrenberg) Simonsen 1979
(Metzeltin and Lange-Bertalot 2007)
- Pl. 66 *Aulacoseira granulata* (Ehrenberg) Simonsen 1979, small form
- Pl. 67-68 *Aulacoseira lacustris* (Grunow in Van Heurck) Krammer 1991
(Camburn and Charles 2000)
- Pl. 69 *Aulacoseira lacustris* (Grunow in Van Heurck) Krammer 1991, robust form
- Pl. 70-73 *Aulacoseira nygaardii* (Camburn) Camburn and Charles 2000
(Siver et al. 2005)
- Pl. 74-79 *Aulacoseira tenella* (Nygaard) Simonsen 1979
(Siver et al. 2005; Camburn and Charles 2000)
- Pl. 80 *Bacillaria* sp. 1
- Pl. 81 *Bacillaria paradoxa* Gmelin in Linnaeus 1788
- Pl. 82-86 *Brachysira brebissonii* Ross in Hartley 1986
(Siver et al. 2005)
- Pl. 87-88 *Brachysira neoacuta* Lange-Bertalot in Lange-Bertalot & Moser 1994
(Lange-Bertalot and Moser 1994)



- Pl. 89-93 *Brachysira microcephala* (Kützing) Compère 1986
(Siver et al. 2005)
- Pl. 94 *Brachysira procera* Lange-Bertalot & Moser 1994
(Lange-Bertalot and Moser 1994)
- Pl. 95-96 *Brachysira serians* (Brébisson) Round & Mann 1981
(Siver et al. 2005; Metzeltin and Lange-Bertalot 2007)
- Pl. 97 *Oxyneis binalis* var. *elliptica* (Flower) Kingston 2000
(Siver et al. 2005)
- Pl. 98-99 *Caloneis bacillum* (Grunow) Cleve 1894
(Siver et al. 2005)
- Pl. 100-102 *Caloneis lewisii* var. *inflata* (Schultze) Patrick 1966
- Pl. 103 *Caloneis jasmineae* Metzeltin & Lange-Bertalot 2007
- Pl. 104-105 *Caloneis thermalis* (Grunow) Krammer in Krammer & Lange-Bertalot 1985
- Pl. 106 *Caloneis ventricosa* (Ehrenberg) Meister 1912
- Pl. 107 *Capartogramma crucicula* (Grunow ex Cleve) Ross 1963
- Pl. 108 *Cavinula cocconeiformis* (Gregory ex Greville) Mann & Stickle in Round, Crawford & Mann 1990
- Pl. 109-112 *Chamaepinnularia* sp. 1
- Pl. 114-115 *Cocconeis fluviatilis* Wallace 1960
- Pl. 117-118 *Cocconeis placentula* Ehrenberg 1838
- Pl. 119 *Cocconeis placentula* Ehrenberg 1838, small form



- Pl. 120 *Craticula* sp. 1
- Pl. 121 *Craticula cuspidata* (Kützing) Mann in Round, Crawford & Mann 1990
- Pl. 122-125 *Cyclotella* sp. 1
- Pl. 126 *Cyclotella* cf. *ocellata* Pantocsek 1902
 (Camburn and Charles 2000)
- Pl. 127-129 *Cyclotella krammeri* Håkansson 1990
- Pl. 130-132 *Cyclotella meneghiniana* Kützing 1844
 (Siver et al. 2005; Camburn and Charles 2000)
- Pl. 133-139 *Cyclotella stelligera* (Cleve & Grunow in Cleve) Van Heurck 1882
 (Siver et al. 2005)
- Pl. 140 *Cymbella cuspidata* Kützing 1844
- Pl. 141 *Cymbella kolbei* var. *angusta* Krammer 2002
 (Krammer 2002)
- Pl. 142-143 *Cymbella peraffinis* Tynni 1978
 (Krammer 2002)
- Pl. 144-145 *Diadesmis confervacea* Kützing 1844
- Pl. 146 *Diploneis parma* Cleve 1891



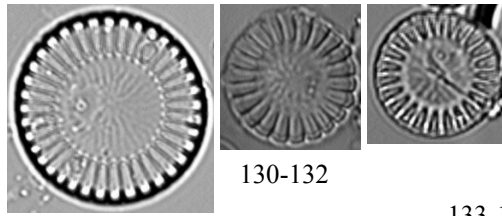
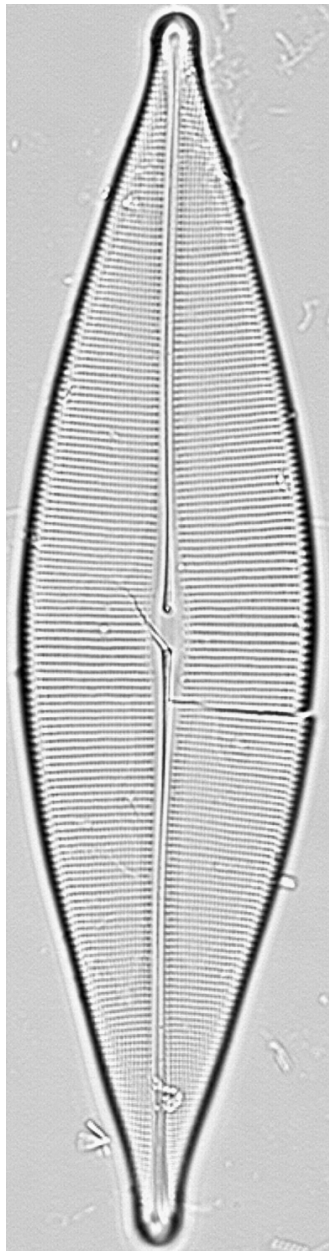
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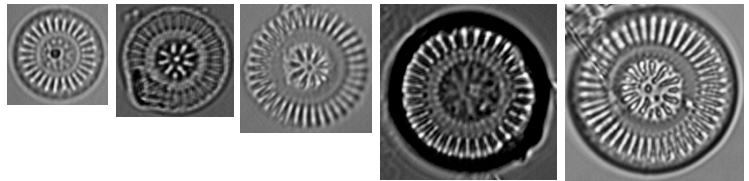
122-125

127-129

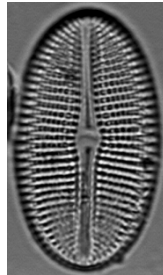


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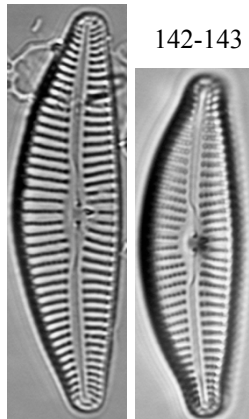
133-139



144-145



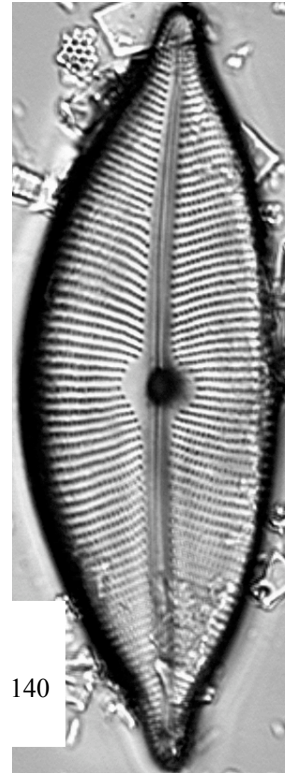
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142-143

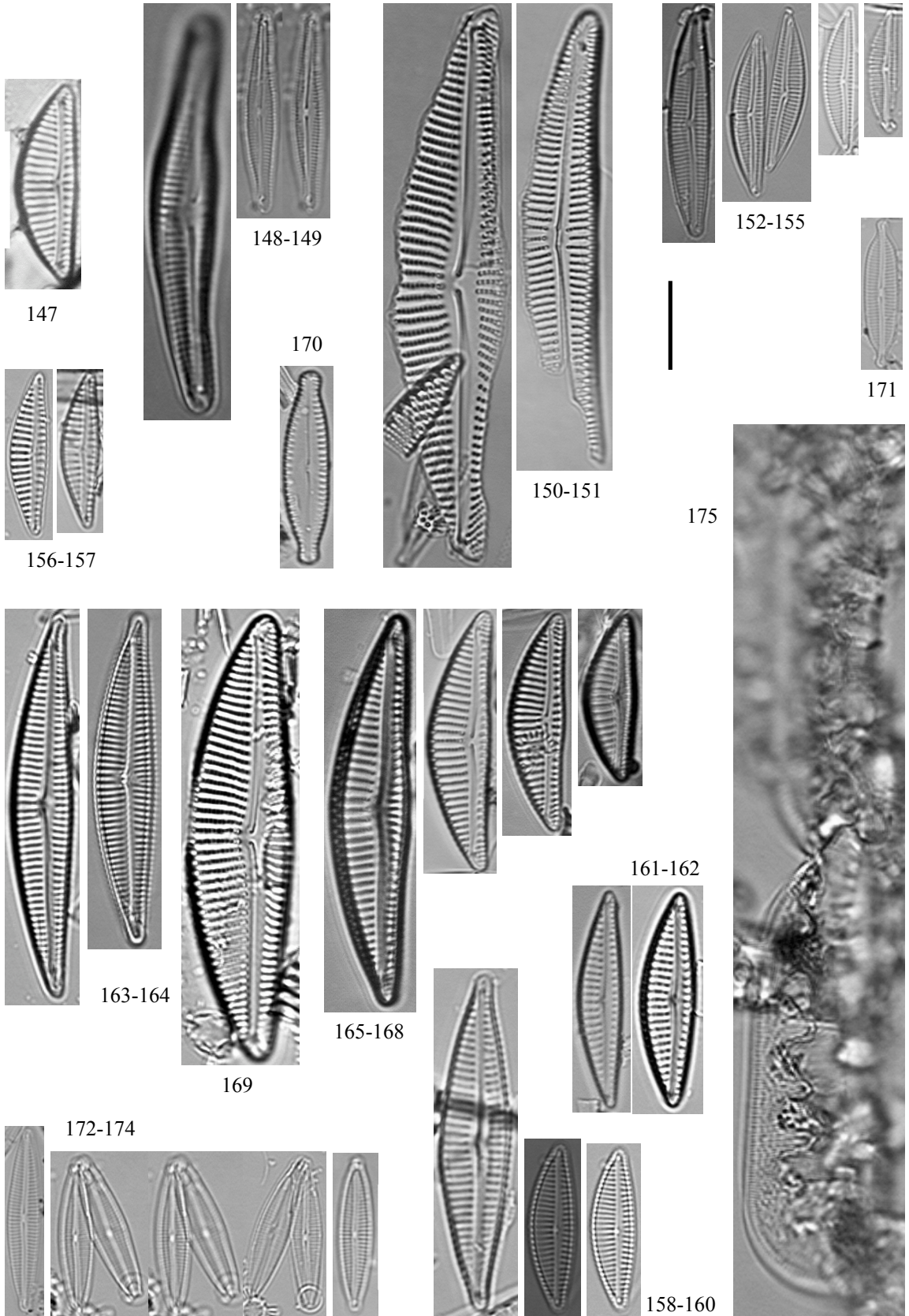


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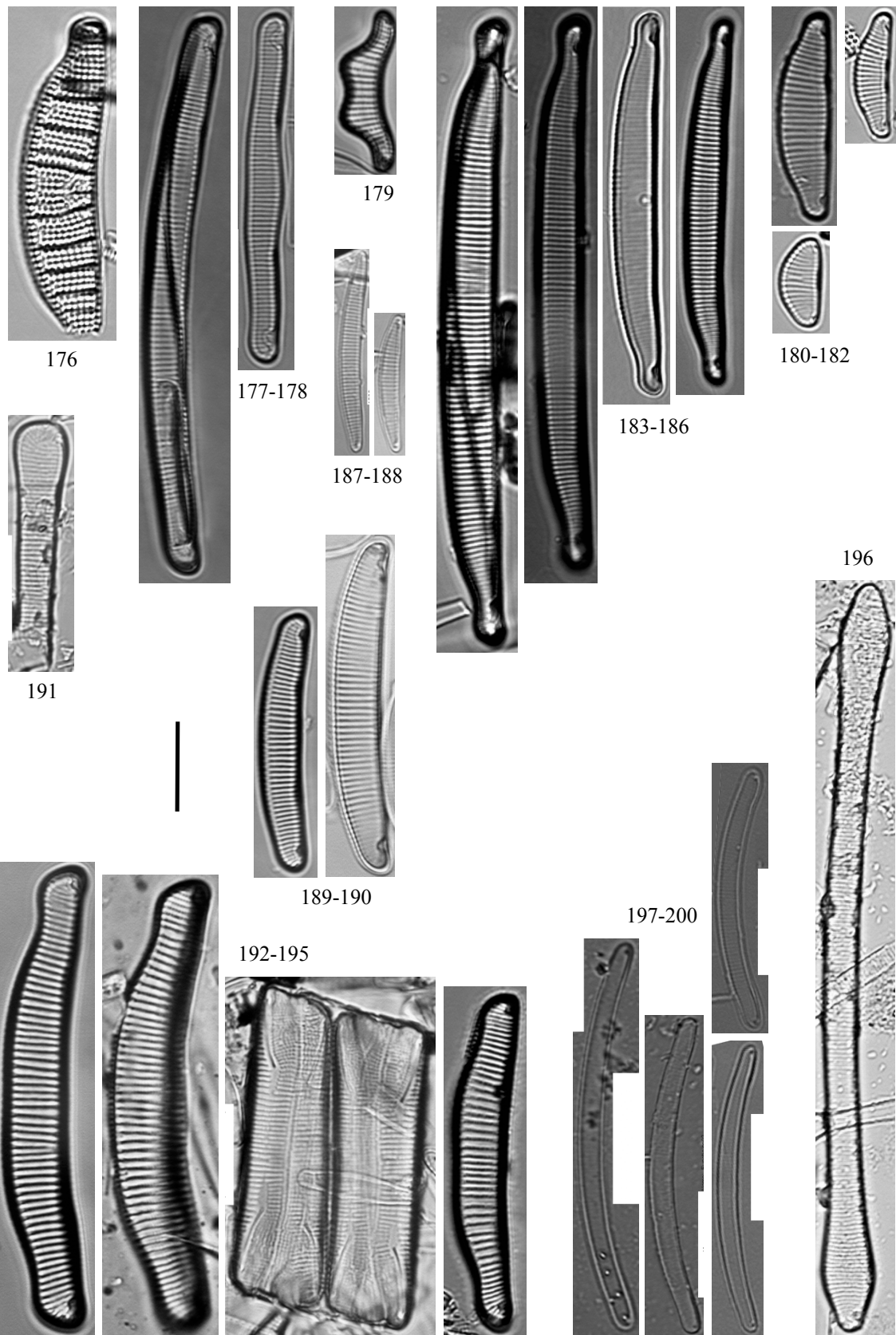


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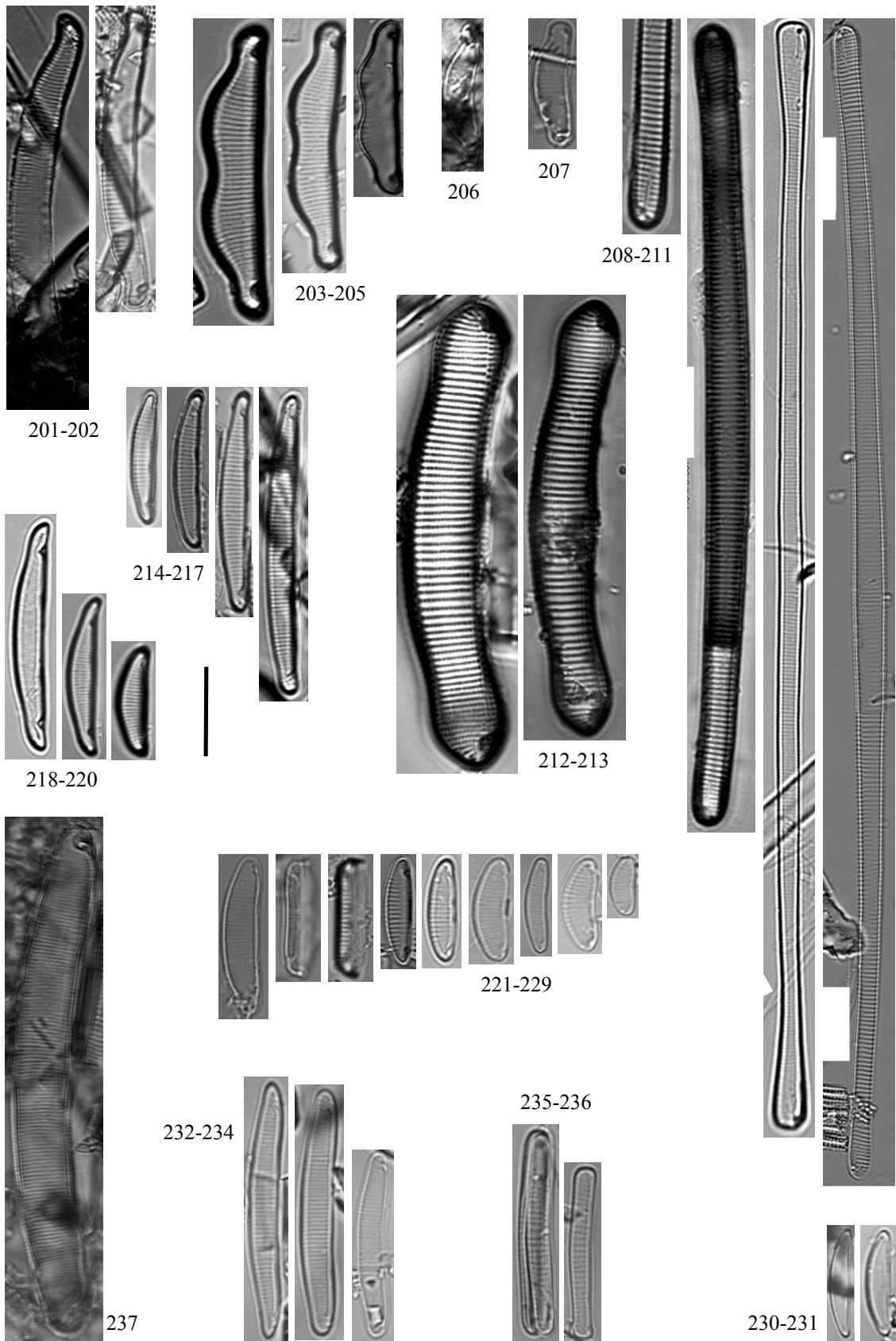
- Pl. 147 *Encyonema minutum* (Hilse in Rabenhorst) Mann in Round, Crawford & Mann 1990
(Siver et al. 2005)
- Pl. 148-149 *Encyonema* (?) sp. 2
- Pl. 150-151 *Encyonema vulgare* Krammer 1997
- Pl. 152-155 *Encyonema evergladianum* Krammer 1997
(Krammer 1997b)
- Pl. 156-157 *Encyonema* sp. 1
- Pl. 158-160 *Encyonema* cf. *gaeumannii* (Meister) Krammer 1997
(Siver et al. 2005)
- Pl. 161-162 *Encyonema subanceolatum* Krammer, Metzeltin et Lange-Bertalot in Krammer 1997
(Metzeltin and Lange-Bertalot 1998)
- Pl. 163-164 *Encyonema neogracile* Krammer 1997
(Krammer 1997a)
- Pl. 165-168 *Encyonema silesiacum* (Bleisch in Rabenhorst) Mann in Round, Crawford & Mann 1990
(Krammer 1997a)
- Pl. 169 *Encyonema silesiacum* (Bleisch in Rabenhorst) Mann in Round, Crawford & Mann 1990, "big" form
- Pl. 170 *Gomphocymbella* (?) sp. 1
- Pl. 171 *Encyonopsis microcephala* (Grunow) Krammer 1997
(Krammer 1997b)
- Pl. 172-174 *Encyonopsis subminuta* Krammer & Reichardt in Krammer 1997
(Krammer 1997b)
- Pl. 175 *Entomoneis ornata* (J. W. Bailey) Reimer in Patrick & Reimer 1975



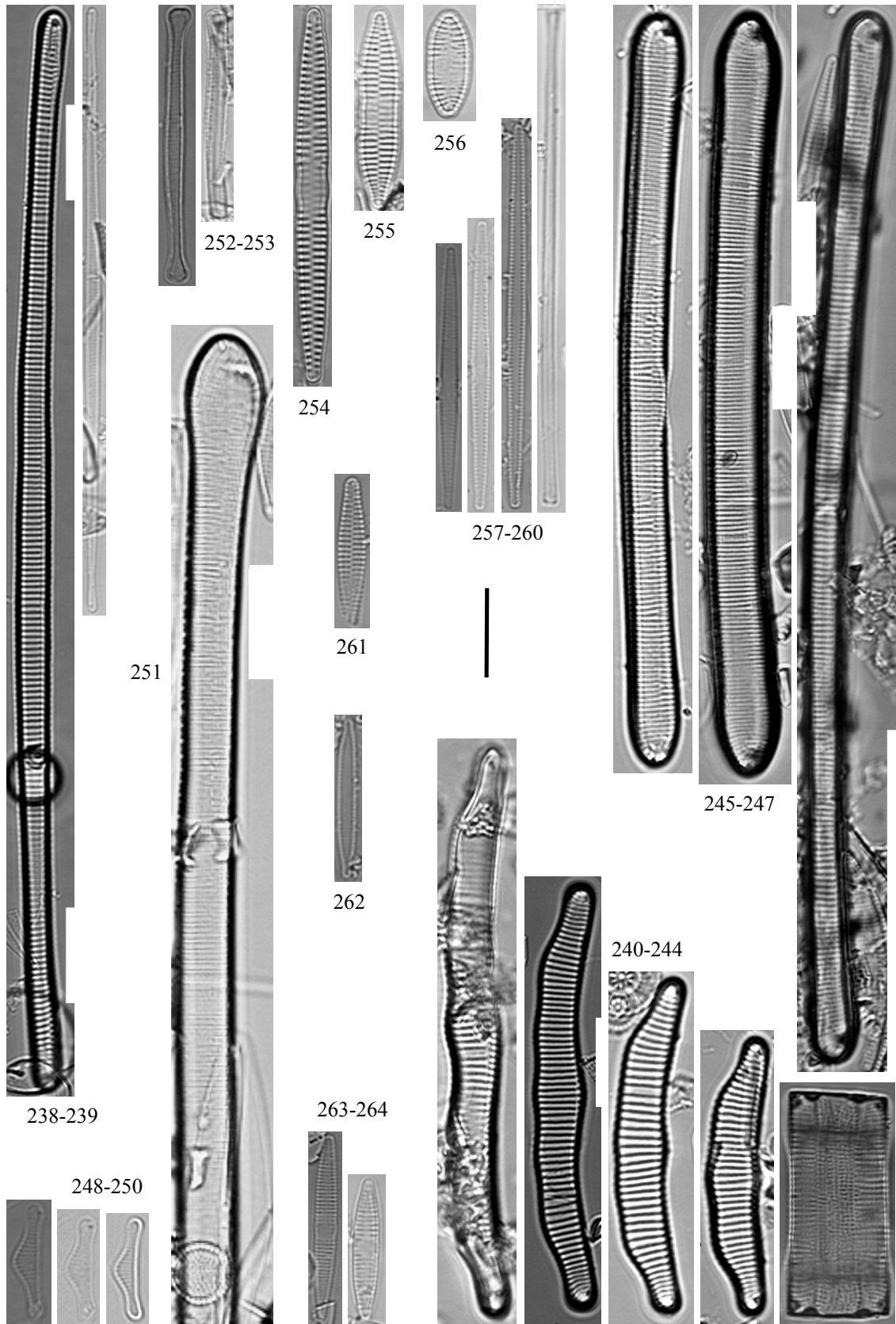
- Pl. 176 *Epithemia adnata* (Kützing) Brébisson 1838
- Pl. 177-178 *Eunotia* sp. 1
- Pl. 179 *Eunotia camelus* Ehrenberg 1843
- Pl. 180-182 *Eunotia carolina* Patrick 1958
(Siver et al. 2005; Camburn and Charles 2000)
- Pl. 183-186 *Eunotia veneris* (Kützing) De Toni 1892
(Metzeltin and Lange-Bertalot 2007)
- Pl. 187-188 *Eunotia curvata* f. *bergii* Woodhead & Tweed 1960
(Siver et al. 2005; Camburn and Charles 2000)
- Pl. 189-190 *Eunotia faba* Ehrenberg 1838
- Pl. 191 *Eunotia femoriformis* (Patrick) Hustedt
(Metzeltin and Lange-Bertalot 2007)
- Pl. 192-195 *Eunotia minor* Fusey 1964
- Pl. 196 *Eunotia transfuga* Metzeltin & Lange-Bertalot 1998, (continued)
(Metzeltin and Lange-Bertalot 1998)
- Pl. 197-200 *Eunotia bilunaris* var. *mucophila* (Naegeli in Kützing) Lange-Bertalot, Norpel & Alles 1991
(Siver et al. 2005)



- Pl. 201-202 *Eunotia denticulata* (Brébisson in Kutzing) Rabenhorst 1864
(Metzeltin and Lange-Bertalot 2007)
- Pl. 203-205 *Eunotia bidentula* W. Smith 1856
(Camburn and Charles 2000)
- Pl. 206 *Eunotia exigua* (Brébisson in Kutzing) Rabenhorst 1864
- Pl. 207 *Eunotia exigua* (Brébisson in Kutzing) Rabenhorst 1864, morph 2
- Pl. 208-211 *Eunotia flexuosa* (Brébisson in Kutzing) Kützing 1849
(Siver et al. 2005; Camburn and Charles 2000)
- Pl. 212-213 *Eunotia formica* Ehrenberg 1843
(Siver et al. 2005; Metzeltin and Lange-Bertalot 1998)
- Pl. 214-217 *Eunotia incisa* W. Smith ex Gregory 1854
(Siver et al. 2005)
- Pl. 218-220 *Eunotia incisa* W. Smith ex Gregory 1854, morph 2
(Camburn and Charles 2000)
- Pl. 221-229 *Eunotia intermedia* (Krasske ex Hustedt) Nörpel & Lange-Bertalot in Lange-Bertalot 1993
(Siver et al. 2005)
- Pl. 230-231 *Eunotia* sp. 2
- Pl. 232-234 *Eunotia* sp. 3
- Pl. 235-236 *Eunotia* sp. 4
- Pl. 237 *Eunotia monodon* Ehrenberg 1843
(Siver et al. 2005)



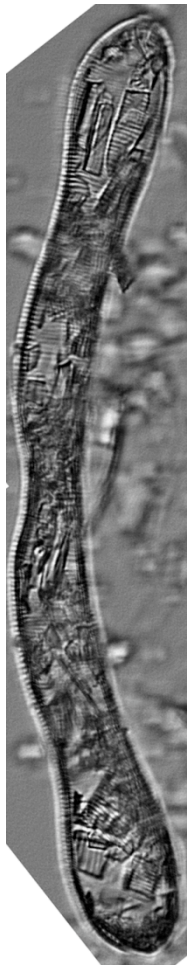
- Pl. 238-239 *Eunotia naegelia* Migula 1907
(Siver et al. 2005)
- Pl. 240-244 *Eunotia pectinalis* (Kützing) Rabenhorst 1864
(Siver et al. 2005)
- Pl. 245-247 *Eunotia rabenhorstiana* (Grunow) Hustedt 1949
(Metzeltin and Lange-Bertalot 2007)
- Pl. 248-250 *Eunotia* sp. 5
- Pl. 251 *Eunotia transfuga* Metzeltin & Lange-Bertalot 1998
(Metzeltin and Lange-Bertalot 1998)
- Pl. 252-253 *Eunotia zasuminensis* (Cabejszekowna) Körner 1970
(Siver et al. 2005; Camburn and Charles 2000)
- Pl. 254 *Fragilaria bidens* Heiberg 1863
- Pl. 255 *Fragilaria bidens* Heiberg 1863, "fat" form
- Pl. 256 *Fragilaria bidens* Heiberg 1863, small form
- Pl. 257-260 *Fragilaria* cf. *nanana* Lange-Bertalot in Krammer & Lange-Bertalot 1991
(Metzeltin and Lange-Bertalot 2007)
- Pl. 261 *Fragilaria* sp. 1
- Pl. 262 *Fragilaria* sp. 2
- Pl. 263-264 *Fragilaria* sp. 3



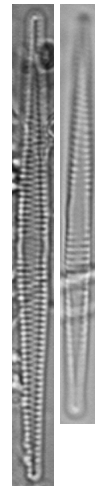
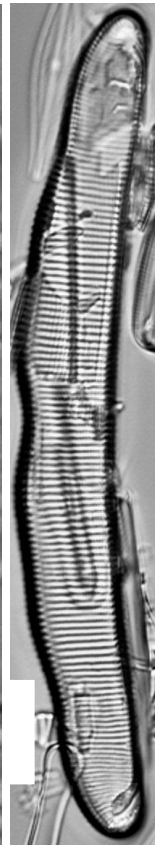
- Pl. 265-267 *Eunotia yanomami* Metzeltin & Lange-Bertalot 1998
(Metzeltin and Lange-Bertalot 1998; Metzeltin and Lange-Bertalot 2007)
- Pl. 268 *Eunotia yanomami* Metzeltin & Lange-Bertalot 1998, long form
(Metzeltin and Lange-Bertalot 1998; Metzeltin and Lange-Bertalot 2007)
- Pl. 269-270 *Fragilaria* sp. 4
- Pl. 271-273 *Fragilaria parasitica* (W. Smith) Heiberg 1863
(Camburn and Charles 2000)
- Pl. 274-275 *Fragilaria rolandschmidtii* Metzeltin & Lange-Bertalot 1998
(Metzeltin and Lange-Bertalot 1998)
- Pl. 277 *Fragilaria synegrotasca* Lange-Bertalot 1993
(Krammer)
- Pl. 277 *Frustulia crassinervia* (Brébisson) Lange-Bertalot & Krammer in Lange-Bertalot & Metzeltin 1996
(Siver et al. 2005; Metzeltin and Lange-Bertalot 2007)
- Pl. 278-279 *Frustulia* cf. *undosa* Metzeltin & Lange-Bertalot 1998
(Metzeltin and Lange-Bertalot 1998; Metzeltin and Lange-Bertalot 2007)
- Pl. 280-282 *Frustulia pseudomagaliesmontana* K.E. Camburn & D.F. Charles 2000
(Siver et al. 2005; Camburn and Charles 2000)
- Pl. 283-284 *Frustulia saxonica* Rabenhorst 1853
(Siver et al. 2005)
- Pl. 285-286 *Gomphonema clavatum* E. Reichardt 1999
(Reichardt 1999)
- Pl. 287-288 *Gomphonema variostriatum* Camburn and Charles 2000
(Camburn and Charles 2000)



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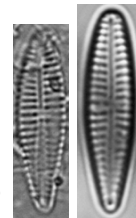
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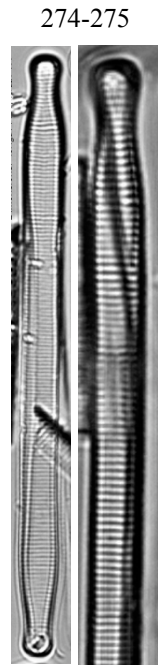
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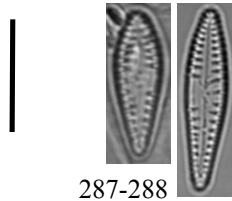
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285-286

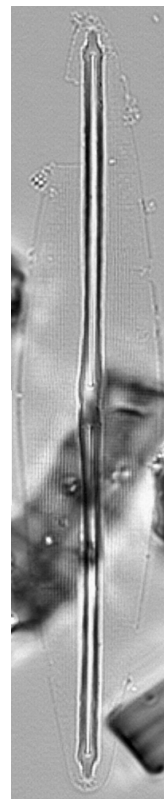
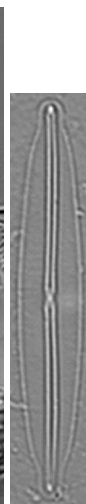
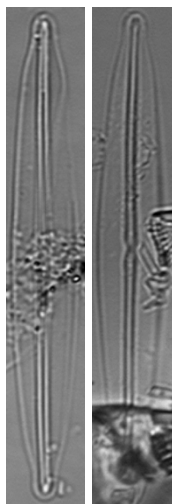


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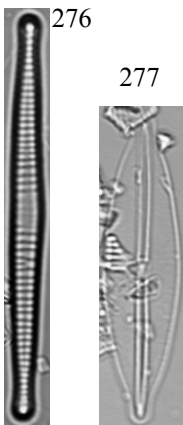


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280-282

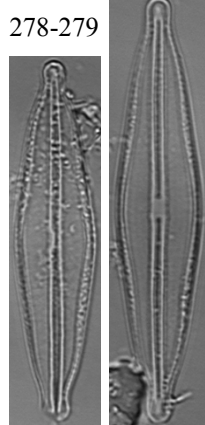


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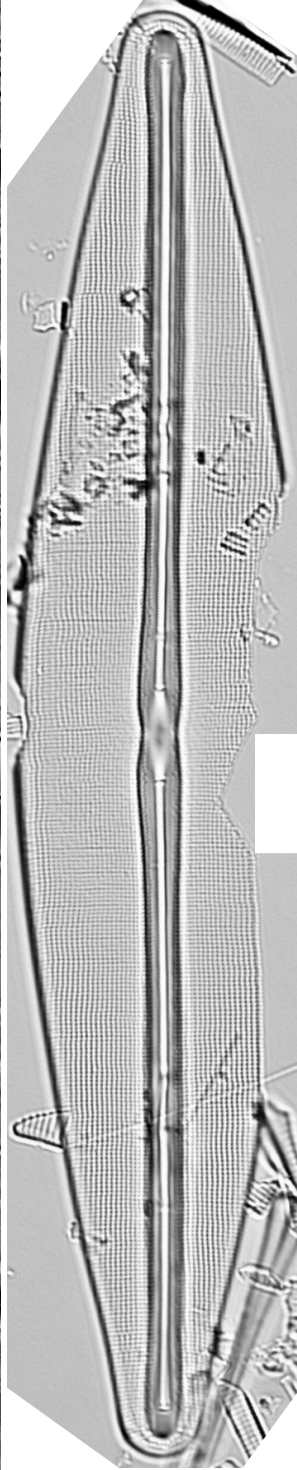
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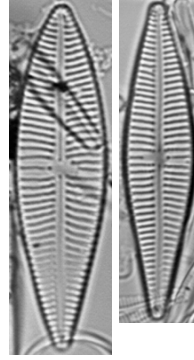


278-279

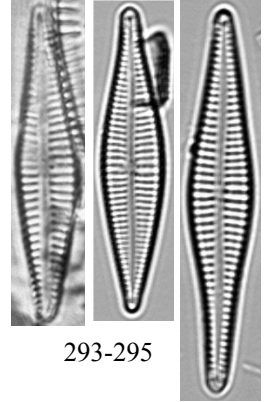
- Pl. 289-290 *Frustulia krammeri* Lange-Bertalot & Metzeltin in Metzeltin & Lange-Bertalot 1998
(Siver et al. 2005)
- Pl. 291-292 *Gomphonema affine* Kützing 1844
(Reichardt 1999)
- Pl. 293-295 *Gomphonema auritum* Braun in litt., Kützing 1849
(Tobias and Gaiser 2006)
- Pl. 296 *Gomphonema coronatum* Ehrenberg 1840
- Pl. 297 *Gomphonema gracile* Ehrenberg 1838
(Tobias and Gaiser 2006)
- Pl. 298 *Gomphonema gracile* Ehrenberg 1838, long form
- Pl. 299 *Gomphonema mexicanum* Grunow in Van Heurck 1880
(Reichardt 1999)
- Pl. 300 *Gomphonema parvulum* (Kützing) Kützing 1849
(Reichardt 1999)
- Pl. 301 *Gomphonema lagenula* Kützing 1844
(Metzeltin and Lange-Bertalot 1998)
- Pl. 302-303 *Gomphonema camburnii* Metzeltin & Lange-Bertalot 1998
(Metzeltin and Lange-Bertalot 1998)
- Pl. 304-305 *Kobayasiella* sp. 1
- Pl. 306-307 *Kobayasiella madumensis* (Jørgensen) Lange-Bertalot 1999
(Siver et al. 2005)



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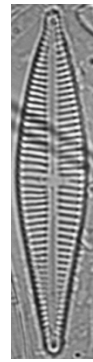
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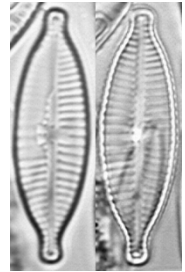


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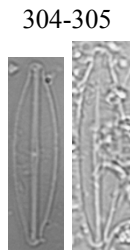


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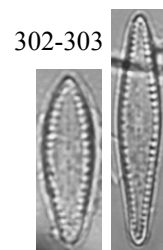
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306-307

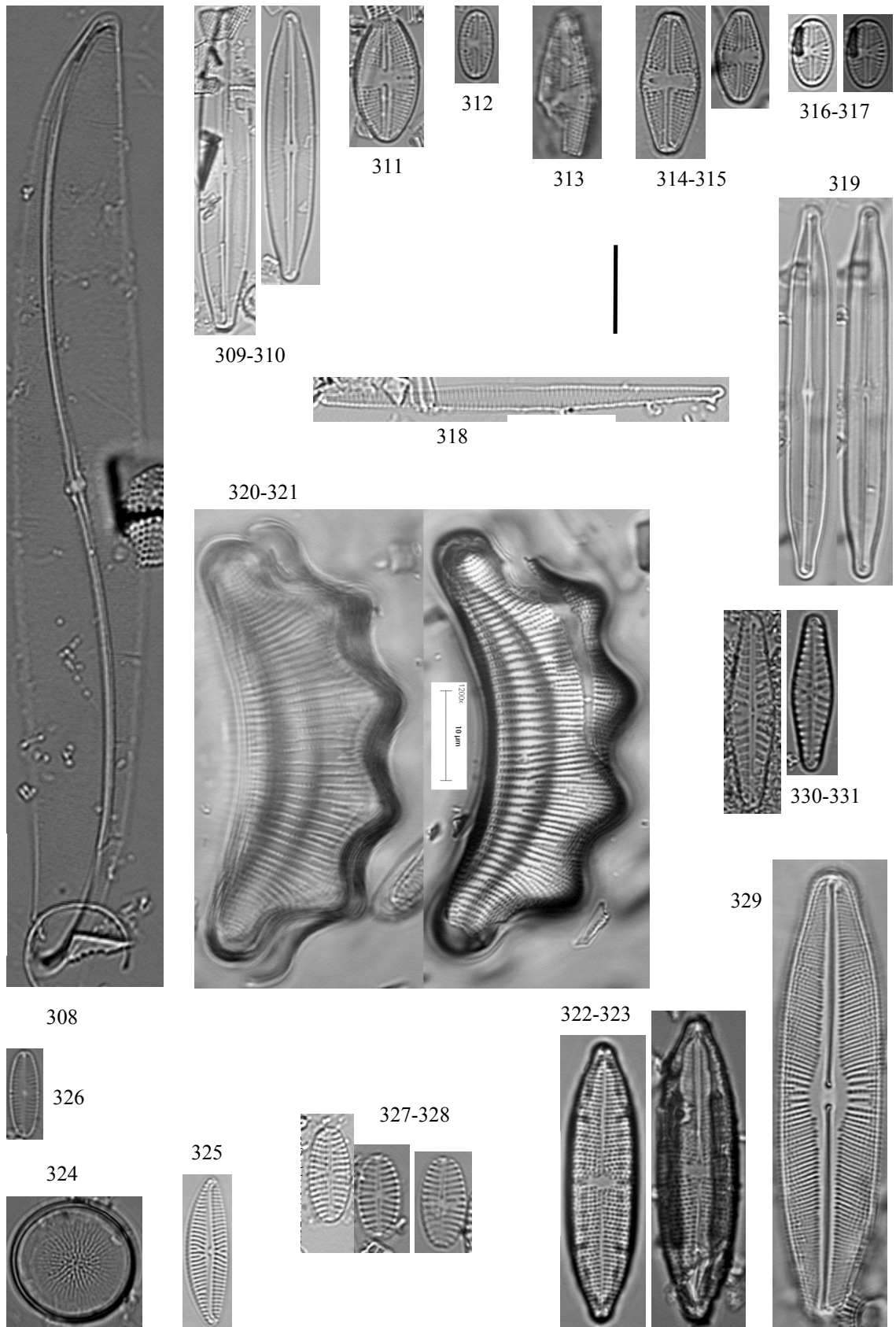


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- Pl. 308 *Gyrosigma obscurum* (W. Smith) Griffith & Henfrey 1856
- Pl. 309-310 *Kobayasiella pseudosubtilissima* (Manguin) Lange-Bertalot 1999
(Siver et al. 2005)
- Pl. 311 *Luticola permuticoides* Metzeltin & Lange-Bertalot 2007
(Metzeltin and Lange-Bertalot 2007)
- Pl. 312 *Luticola* sp. 1
- Pl. 313 *Luticola goeppertiana* (Bleisch in Rabenhorst) Mann in Round, Crawford & Mann 1990
- Pl. 314-315 *Luticola* sp. 2
- Pl. 316-317 *Luticola saxophila* (Bock ex Hustedt) Mann in Round, Crawford & Mann in Round, Crawford & Mann 1990
- Pl. 318 *Fragilaria capucina* var. *gracilis* (Østrup) Hustedt 1950
- Pl. 319 *Kobayasiella* sp. 2
- Pl. 320-321 *Eunotia serra* var. *diadema* (Ehrenberg) Patrick 1958
(Siver et al. 2005)
- Pl. 322-323 *Mastogloia smithii* Thwaites in lit. ex W. Smith 1856
- Pl. 324 cf. *Brevisira arentii* (Kolbe) Krammer 2001
- Pl. 325 *Navicella pusilla* (Grunow) Krammer 1997
- Pl. 326 *Navicula* cf. *agrestis* Hustedt 1937
- Pl. 327-328 *Navicula* cf. *submuralis* Hustedt 1945
- Pl. 329 *Navicula brasiliana* (Cleve) Cleve 1894
- Pl. 330-331 *Navicula capitata* var. *lueneburgensis* (Grunow) Patrick in Patrick & Reimer 1966



- Pl. 332 *Navicula* sp. 1
- Pl. 333 *Navicula* cf. *agrestis* Hustedt 1937
- Pl. 334-335 *Navicula* cf. *seminulum* Grunow 1860
- Pl. 336 *Navicula* cf. *similis* Krasske 1929
- Pl. 337-338 *Navicula wildii* Lange-Bertalot 1993
- Pl. 339 *Navicula cincta* (Ehrenberg) Ralfs in Pritchard 1861
- Pl. 340 *Navicula clementis* Grunow 1882
- Pl. 341 *Navicula clementis* Grunow 1882, morph 2
- Pl. 342-343 *Navicula constans* Hustedt 1944
- Pl. 344-347 *Navicula cryptocephala* Kützing 1844
(Siver et al. 2005)
- Pl. 348 *Navicula gradata* Hustedt 1937
- Pl. 349 *Navicula elginensis* (Gregory) Ralfs in Pritchard 1861
- Pl. 350 *Navicula gastrum* (Ehrenberg) Kützing 1844
- Pl. 351 *Navicula* sp. 3
- Pl. 352-353 *Navicula* sp. 4
- Pl. 354 *Navicula* sp. 7
- Pl. 355 *Navicula* sp. 5
- Pl. 356-357 *Navicula molestiformis* Hustedt 1949
- Pl. 358 *Navicula notha* Wallace 1960
(Siver et al. 2005)
- Pl. 359 *Navicula protracta* (Grunow in Cleve & Grunow) Cleve 1894



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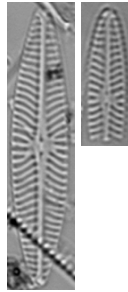
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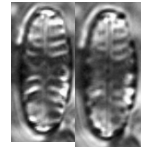
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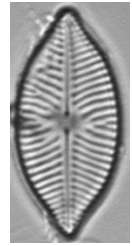
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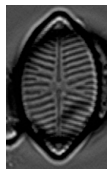
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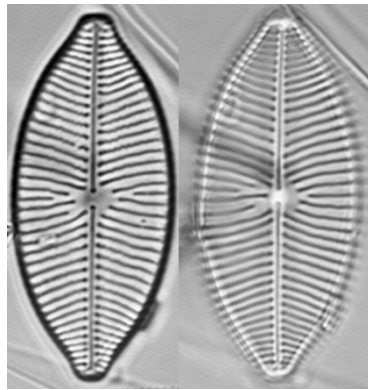
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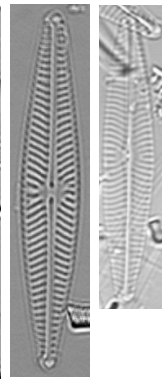
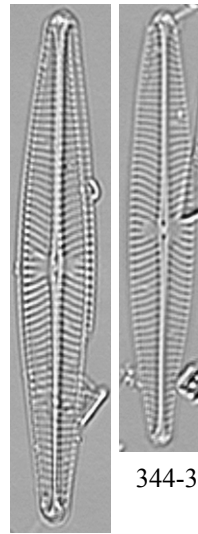
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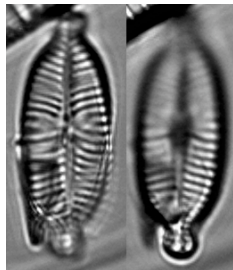
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344-347



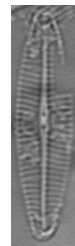
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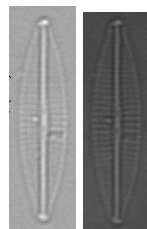
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356-357



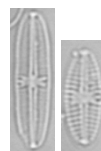
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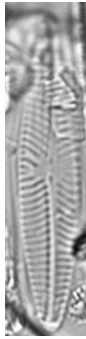
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352-353



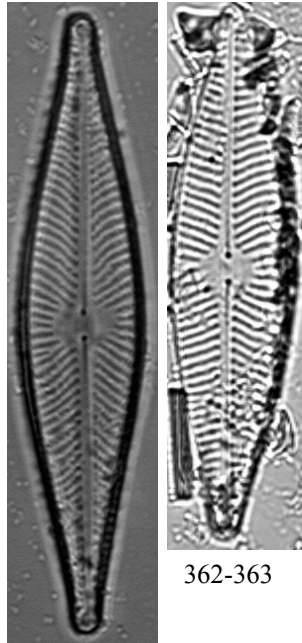
- Pl. 360 *Navicula* sp. 6
- Pl. 361 *Navicula subrhynchocephala* Hustedt 1935
- Pl. 362-363 *Navicula trivialis* Lange-Bertalot 1980
- Pl. 364 *Navicula* sp. 8
- Pl. 365-366 *Neidium* cf. *alpinum* var. *quadripunctatum* (Hustedt) Hamilton in Hamilton, Poulin & Taylor 1990
(Siver et al. 2005; Camburn and Charles 2000)
- Pl. 367 *Neidium* cf. *alpinum* var. *quadripunctatum* (Hustedt) Hamilton in Hamilton, Poulin & Taylor 1990, long form
- Pl. 368 *Neidium amphigomphus* (Ehrenberg) Pfitzer 1871
(Siver et al. 2005)
- Pl. 369-372 *Neidium ampliatum* (Ehrenberg) Krammer in Krammer & Lange-Bertalot 1985
(Siver et al. 2005)
- Pl. 373-374 *Neidium amphirhynchus* (Ehrenberg) Pfitzer 1871
(Camburn and Charles 2000)
- Pl. 375-376 *Neidium densestriatum* (Østrup) Krammer in Krammer & Lange-Bertalot 1985
(Siver et al. 2005)
- Pl. 377-379 *Nitzschia amphibia* Grunow 1862
(Siver et al. 2005)
- Pl. 380 *Nitzschia amphibia* Grunow 1862, morph 2



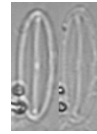
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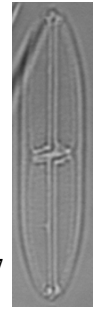
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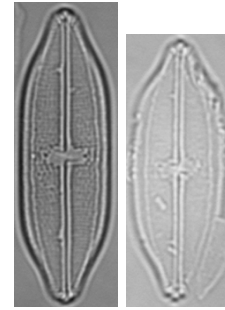
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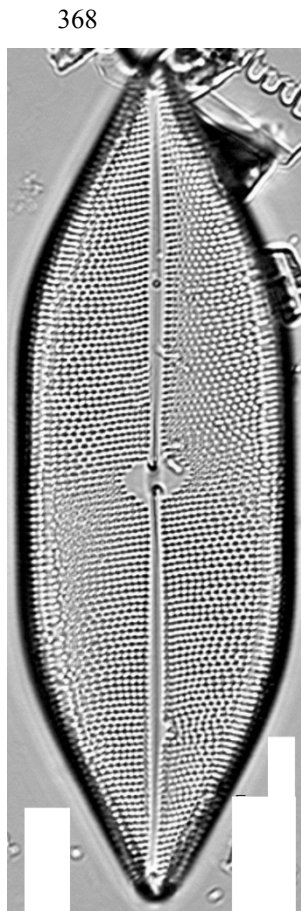
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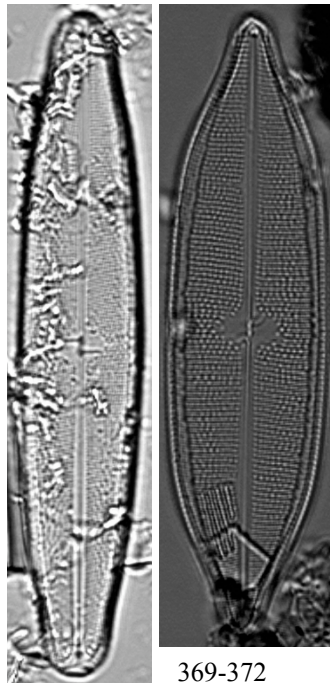
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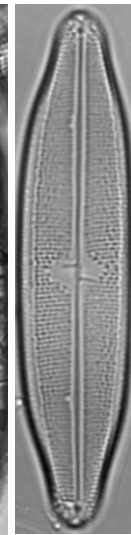
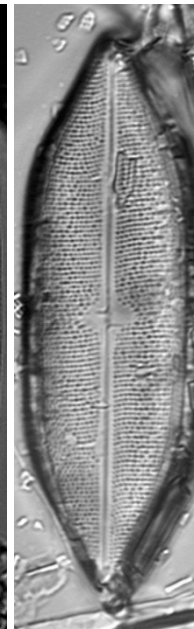
373-374



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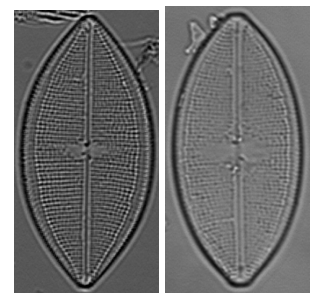
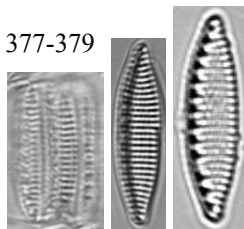
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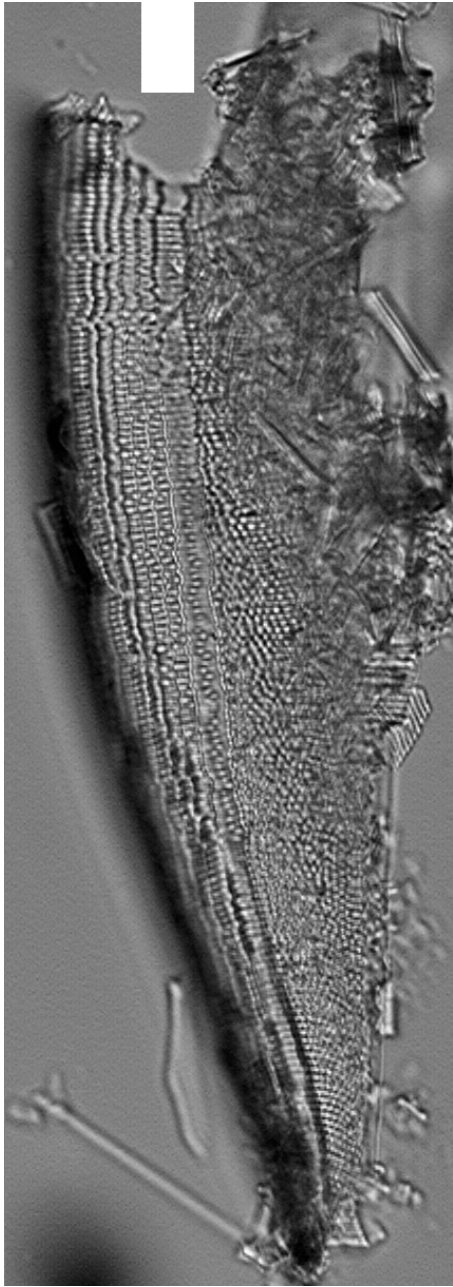


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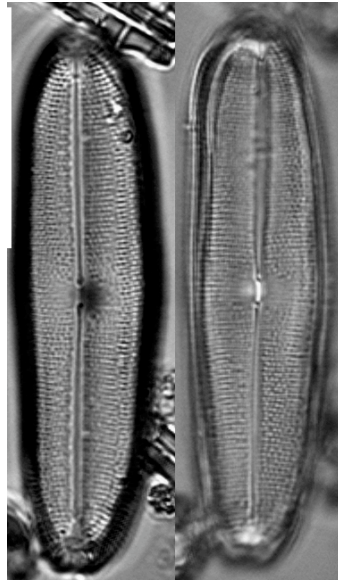


375-376

- Pl. 381 *Neidium tumescens* (Grunow in Schmidt & al.) Cleve 1894
(Metzeltin and Lange-Bertalot 2007)
- Pl. 382 *Neidium cf. hercynicum* Mayer 1915
- Pl. 383 *Neidium floridanum* Reimer 1959
- Pl. 384 *Neidium saccoense* Reimer 1966
- Pl. 385 *Nitzschia cf. acidoclinata* Lange-Bertalot 1976
- Pl. 386 *Nitzschia cf. acidoclinata* Lange-Bertalot 1976, large form
- Pl. 387 *Navicula viridula* (Kützing) Ehrenberg 1838
- Pl. 388 *Nitzschia cf. capitellata* Hustedt in Schmidt & al. 1922
- Pl. 389 *Nitzschia cf. inconspicua* Grunow 1862
- Pl. 390 *Nitzschia cf. perminuta* (Grunow in Van Heurck) Peragallo 1903
- Pl. 391 *Nitzschia cf. pura* Hustedt 1954
- Pl. 392-393 *Nitzschia frustulum* (Kützing) Grunow in Cleve & Grunow 1880
- Pl. 394 *Nitzschia gracilis* Hantzsch 1860



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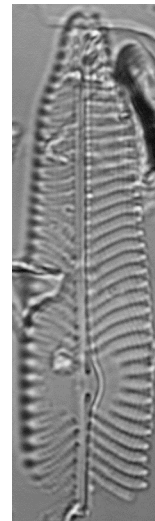
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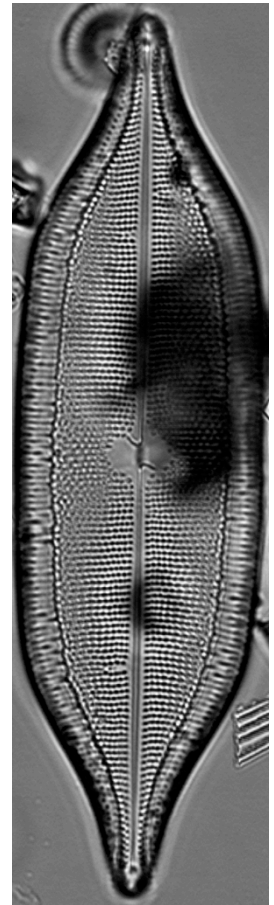
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392-393



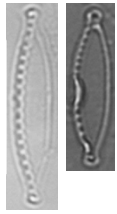
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- Pl. 395-396 *Nitzschia* sp. 1
- Pl. 397 *Nitzschia* sp. 2
- Pl. 398 *Nitzschia* sp. 3
- Pl. 399 *Tryblionella salinarum* (Grunow in Cleve & Grunow) Pelletan 1889
- Pl. 400 *Tryblionella victoriae* Grunow 1862
- Pl. 401 *Nitzschia nana* Grunow in Van Heurck 1881
(Siver et al. 2005)
- Pl. 402 *Nitzschia palea* (Kützing) W. Smith 1856
- Pl. 403 *Nitzschia palea* var. *debilis* (Kützing) Grunow in Cleve & Grunow 1880
(Siver et al. 2005)
- Pl. 404 *Nitzschia paleacea* (Grunow in Cleve & Grunow) Grunow in Van Heurck 1881
- Pl. 405 *Neidium ampliatum* (Ehrenberg) Krammer in Krammer & Lange-Bertalot 1985, small form
- Pl. 406 *Nitzschia scalaris* (Ehrenberg) W. Smith 1853
- Pl. 407-409 *Nitzschia semirobusta* Lange-Bertalot 1993
- Pl. 410 *Nitzschia sigma* (Kützing) W. Smith 1853
- Pl. 411-412 *Nupela* sp. 1
- Pl. 413 *Nupela* cf. *chilensis* (Krasske) Lange-Bertalot in Lange-Bertalot & Moser 1994
- Pl. 414-416 *Nupela* cf. *rumrichorum* Lange-Bertalot in Lange-Bertalot & Moser 1994
- Pl. 417-419 *Nupela neotropica* Lange-Bertalot in Lange-Bertalot & Moser 1994
(Siver et al. 2005)
- Pl. 420-422 *Peronia heribaudi* Brun & Peragallo in Heribaud 1893
(Camburn and Charles 2000)

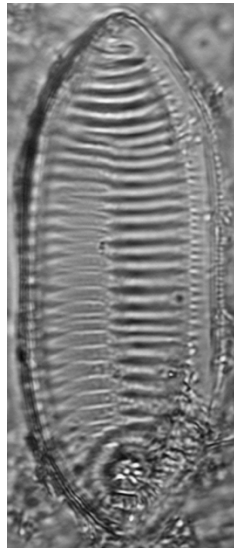


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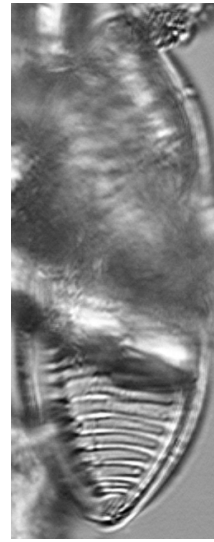


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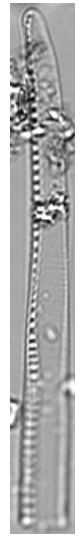
395 - 396



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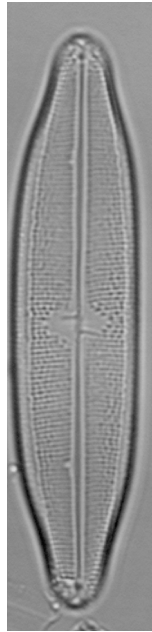
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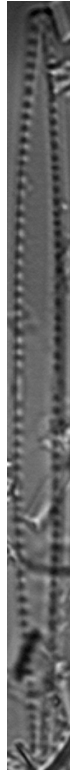
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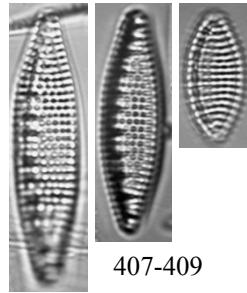
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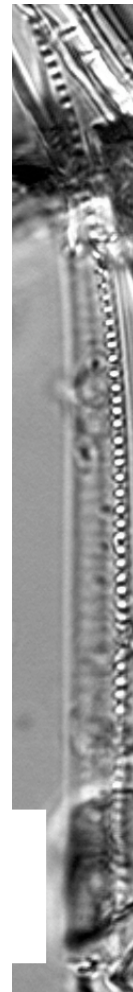


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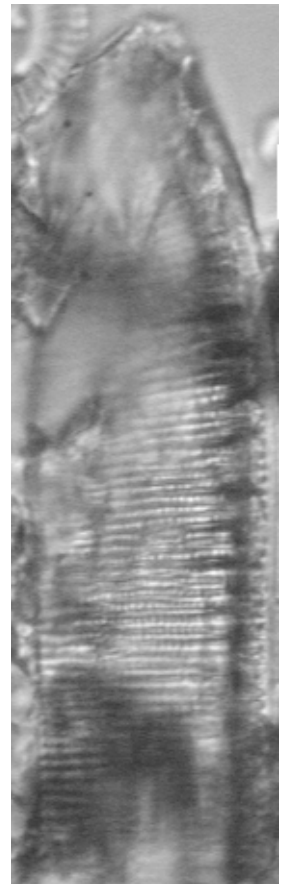


407-409

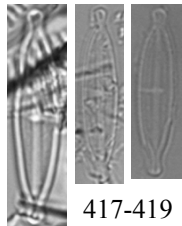
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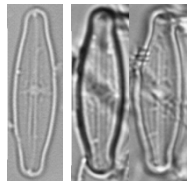
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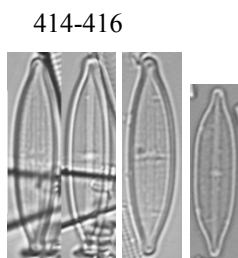
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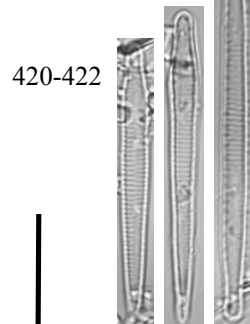
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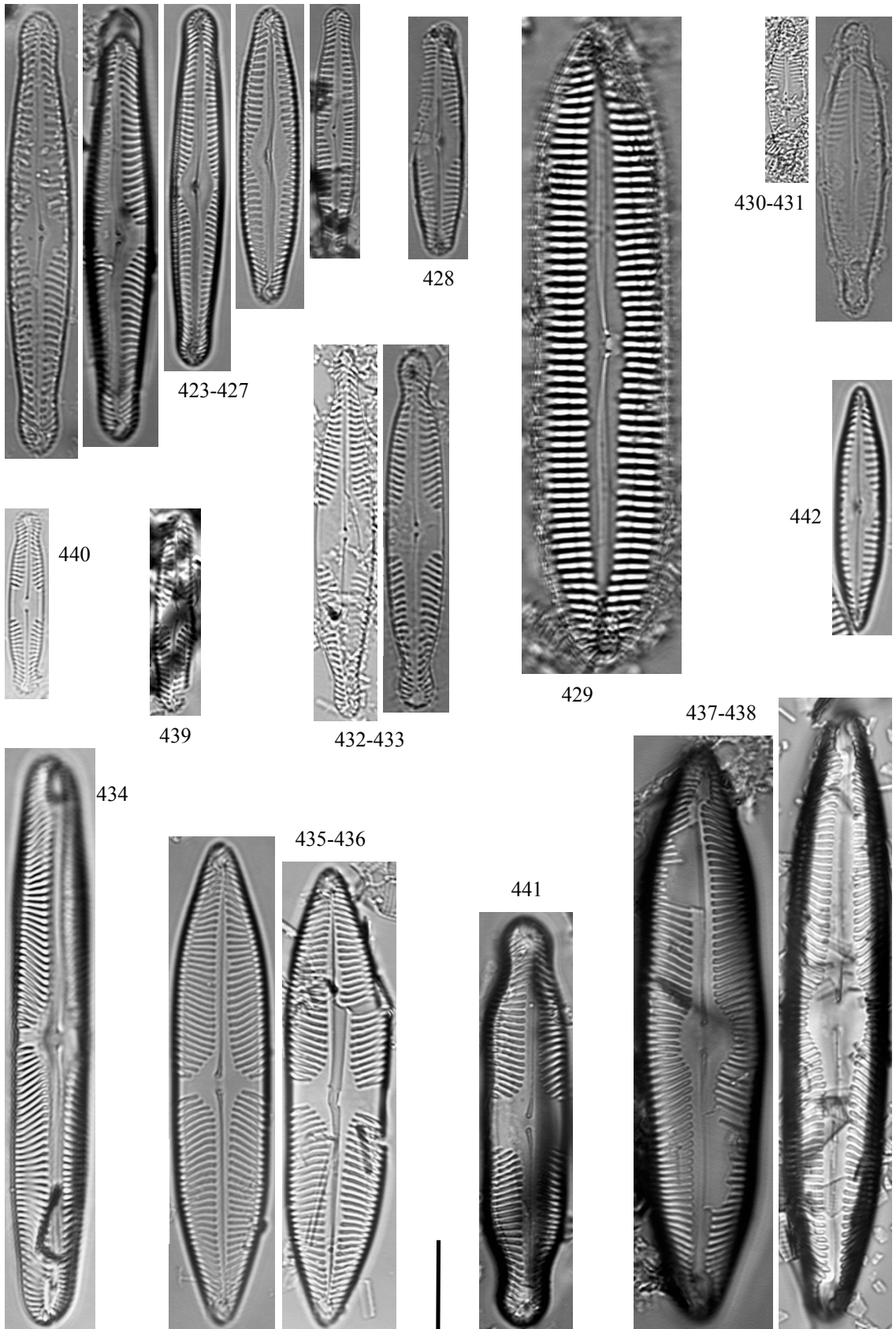


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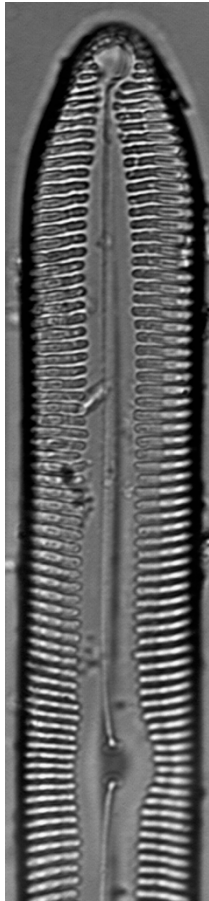
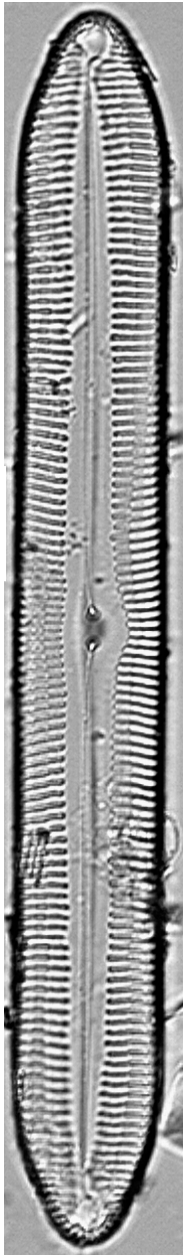


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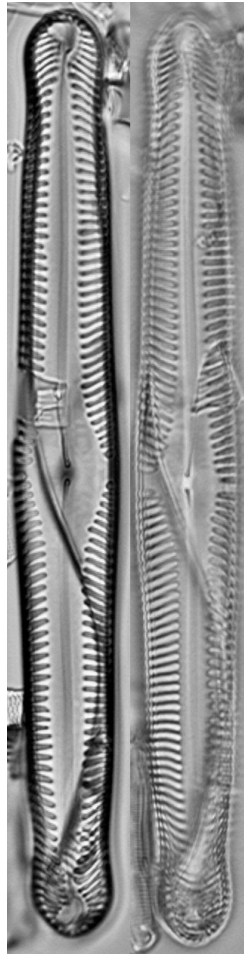
- Pl. 423-427 *Pinnularia amabilis* Krammer 2000
(Krammer 2000)
- Pl. 428 *Pinnularia appendiculata* (Agardh) Cleve 1895
- Pl. 429 *Pinnularia* sp. 1
- Pl. 430-431 *Pinnularia brauniana* (Grunow) Mills 1934
(Metzeltin and Lange-Bertalot 1998)
- Pl. 432-433 *Pinnularia brauniana* (Grunow) Mills 1934, morph 2
- Pl. 434 *Pinnularia* sp. 2
- Pl. 435-436 *Pinnularia balatonis* (Pantocsek) Mills 1934
(Krammer 2000)
- Pl. 437-438 *Pinnularia tumescens* Metzeltin & Krammer in Metzeltin & Lange-Bertalot 1998
(Metzeltin and Lange-Bertalot 1998; Metzeltin and Lange-Bertalot 2007)
- Pl. 439 *Pinnularia* cf. *divergentissima* (Grunow in Van Heurck) Cleve 1895
- Pl. 440 *Pinnularia* cf. *schroeterae* Krammer 2000
- Pl. 441 *Pinnularia* cf. *subanglica* Krammer 2000
(Siver et al. 2005)
- Pl. 442 *Pinnularia* sp. 4



- Pl. 443-444 *Pinnularia* cf. *magnacuneata* Krammer 2000
(Krammer 2000)
- Pl. 445-447 *Pinnularia gibba* Ehrenberg
(Krammer 2000)
- Pl. 448 *Pinnularia gibbiformis* Krammer 1992
(Siver et al. 2005)
- Pl. 449 *Pinnularia* sp. 5
- Pl. 450 *Pinnularia* cf. *lata* (Brébisson) W. Smith 1853
(Krammer 2000)
- Pl. 451-454 *Pinnularia microstauron* (Ehrenberg) Cleve 1891
(Metzeltin and Lange-Bertalot 1998)
- Pl. 455-457 *Pinnularia oominensis* Kobayasi in Yamagishi & Kobayasi 1971, morph 2



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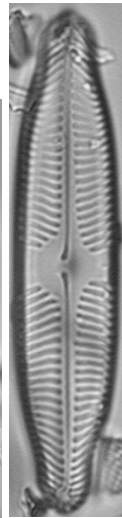
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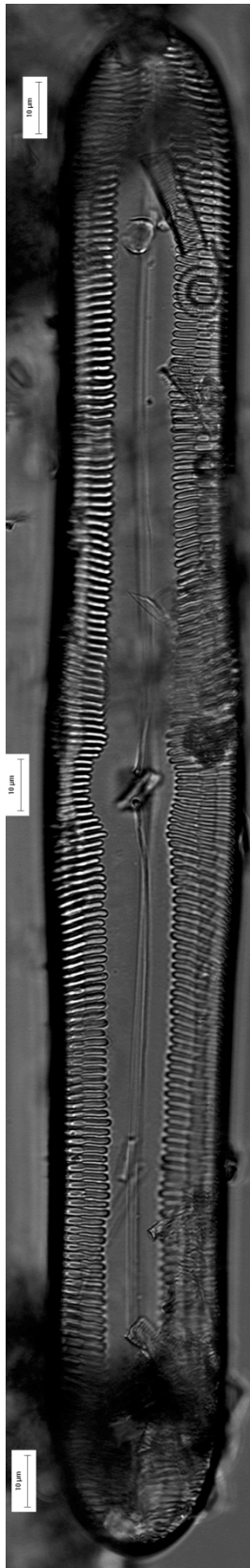
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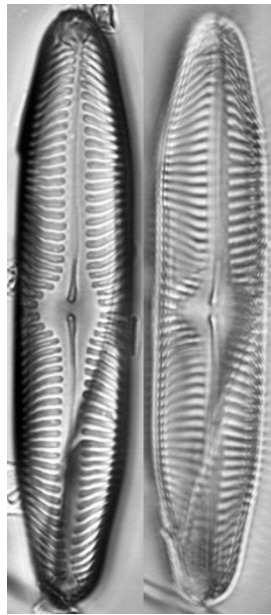
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- Pl. 458 *Pinnularia maior* (Kützing) Rabenhorst
- Pl. 459 *Pinnularia microstauron* var. *nonfasciata* (Ehrenberg) Cleve 1891
(Siver et al. 2005)
- Pl. 460 *Pinnularia microstauron* var. *rostrata* Krammer 2000
- Pl. 461-465 *Pinnularia oominensis* Kobayasi in Yamagishi & Kobayasi 1971
(Metzeltin and Lange-Bertalot 2007)
- Pl. 466 *Pinnularia percuneata* Krammer 2000
(Krammer 2000)
- Pl. 467-468 *Pinnularia schroeterae* var. *elliptica* Krammer 2000
(Krammer 2000)
- Pl. 469 *Pinnularia* sp. 6
- Pl. 470 *Pinnularia* sp. 7
- Pl. 471-473 *Pinnularia viridis* (Nitzsch) Ehrenberg 1843
(Siver et al. 2005)



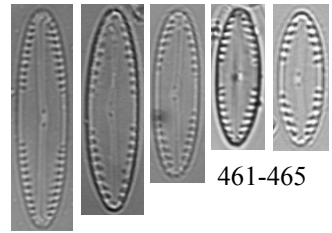
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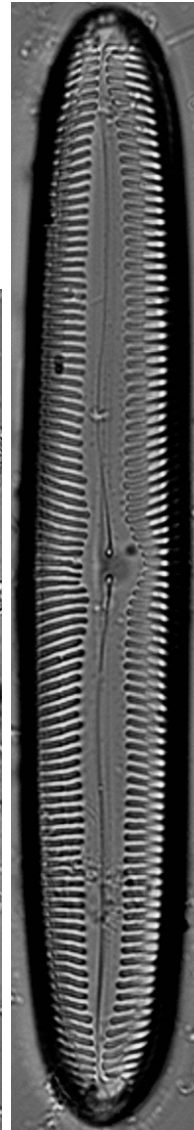
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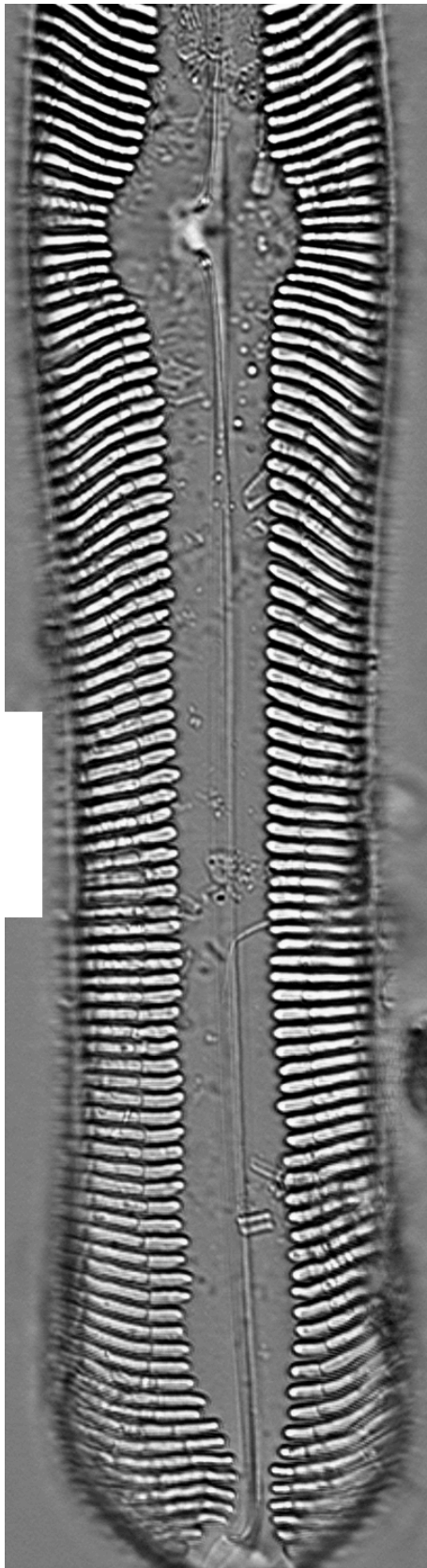
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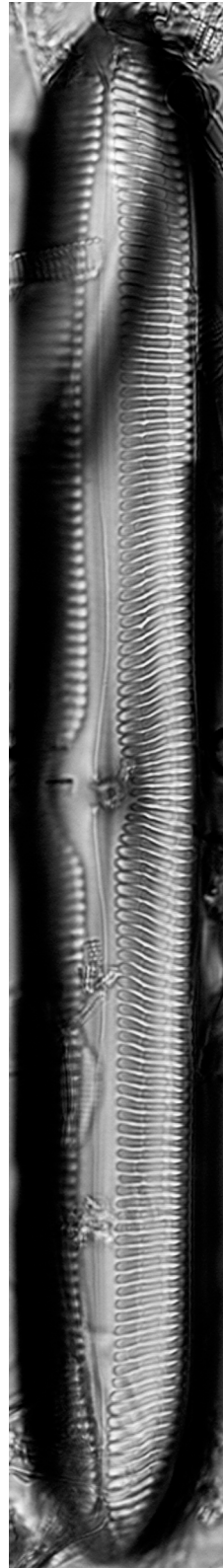
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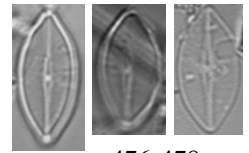
- Pl. 474 *Pinnularia pulchella* (Boyer) Krammer 2000
- Pl. 475 *Pinnularia viridis* (Nitzsch) Ehrenberg 1843, (continued)
(Siver et al. 2005)
- Pl. 476-478 *Planothidium* sp. 1
- Pl. 479-481 *Planothidium apiculatum* (Patrick) Lange-Bertalot 1999
- Pl. 482-483 *Planothidium* sp. 2
- Pl. 484 *Planothidium* sp. 3
- Pl. 485-486 *Planothidium* sp. 4
- Pl. 487-488 *Planothidium* sp. 5
- Pl. 489-490 *Pseudostaurosira* sp. 1
- Pl. 491 *Pinnularia neomajor* Krammer 1992
(Krammer 2000)
- Pl. 492 *Sellaphora* aff. *pupula* (Kützing) Mereschkowsky 1902



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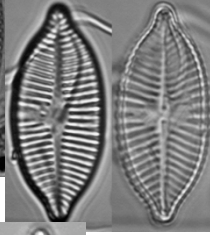
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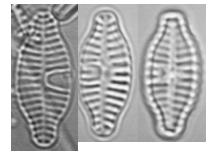
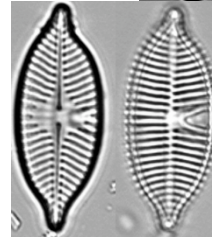
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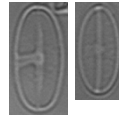
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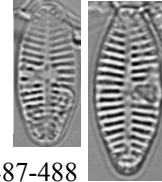
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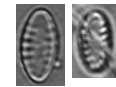
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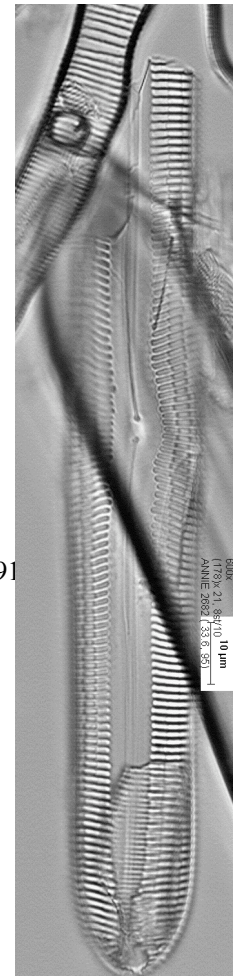
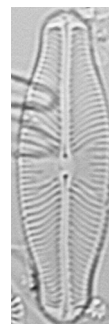


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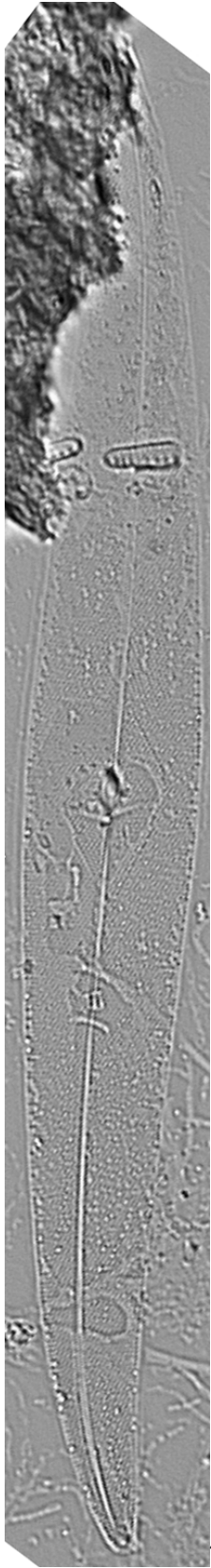
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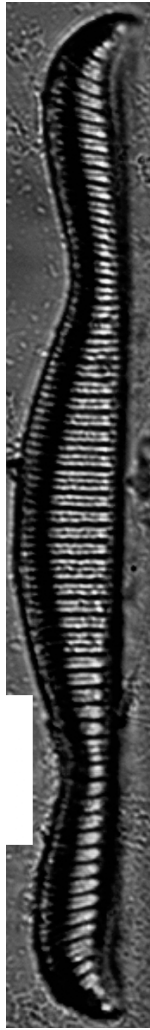
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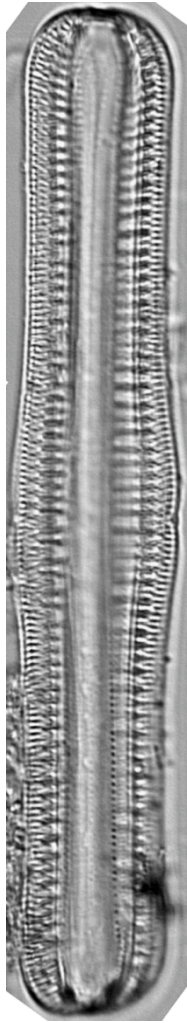
- Pl. 493 *Pleurosigma salinarum* (Grunow) Grunow in Cleve & Grunow 1880
- Pl. 494-496 *Rhopalodia gibba* (Ehrenberg) Otto Müller 1895
- Pl. 497-498 *Rhopalodia gibberula* (Ehrenberg) Otto Müller 1895
- Pl. 499 *Sellaphora* sp. 1
- Pl. 500 *Sellaphora* sp. 2
- Pl. 501-502 *Sellaphora pupula* (Kützing) Mereschkowsky 1902
(Siver et al. 2005)
- Pl. 503 *Stauroneis anceps* Ehrenberg 1843
- Pl. 504-505 *Stauroneis acidobionta* Lange-Bertalot & Wydrzycka 2001
(Metzeltin and Lange-Bertalot 2007)
- Pl. 506 *Stauroneis* sp. 2
- Pl. 507-508 *Stauroneis pachycephala* Cleve 1881
(Metzeltin and Lange-Bertalot 2007)
- Pl. 509-513 *Staurosira venter* (Ehrenberg) Grunow in Pantocsek 1889
(Siver et al. 2005)
- Pl. 514-515 *Staurosira venter* (Ehrenberg) Grunow in Pantocsek 1889, morph 2
- Pl. 516-519 *Staurosira venter* (Ehrenberg) Grunow in Pantocsek 1889, long form



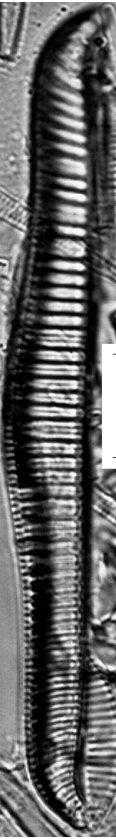
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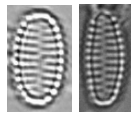
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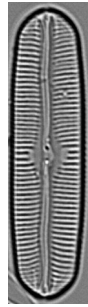
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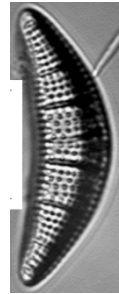
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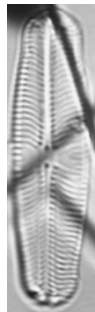
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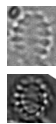
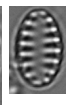
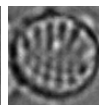
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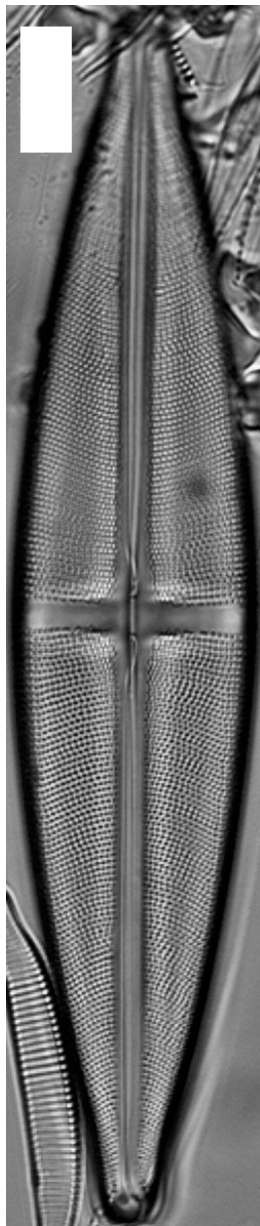
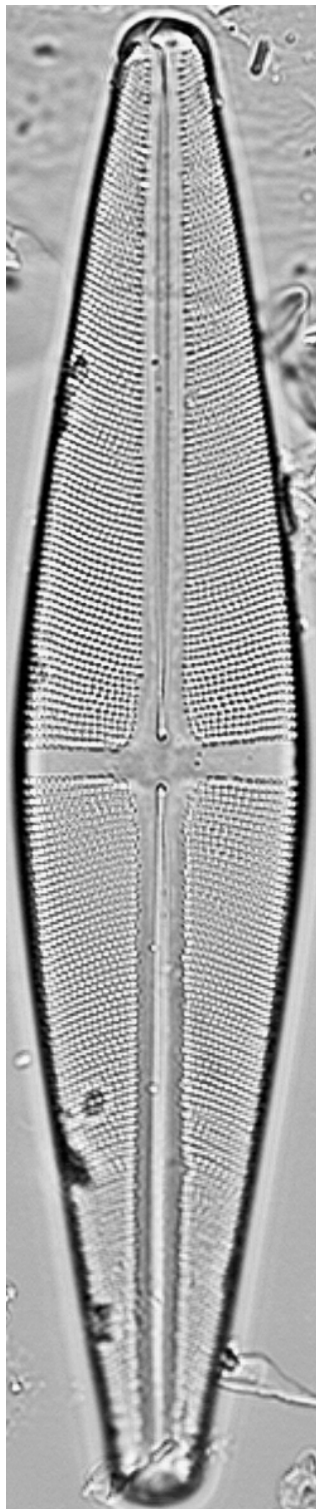


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- Pl. 520-522 *Stauroneis phoenicenteron* (Nitzsch) Ehrenberg 1843
(Siver et al. 2005)
- Pl. 523 *Stauroneis staurolineata* Reimer 1961
(Siver et al. 2005)
- Pl. 524-528 *Stausosira venter* (Ehrenberg) Grunow in Pantocsek 1889, medium form
- Pl. 529 *Stausosira venter* (Ehrenberg) Grunow in Pantocsek 1889, pinched form
- Pl. 530 *Stausosirella* sp. 1
- Pl. 531-534 *Stausosirella pinnata* (Ehrenberg) Williams & Round 1987
(Siver et al. 2005)
- Pl. 535 *Sellaphora* cf. *rectangularis* (Gregory) Lange-Bertalot & Metzeltin 1996
- Pl. 536 *Stausosirella pinnata* var. *lancettula* (Schumann) Siver & Hamilton in Siver & al. 2005
- Pl. 537-538 *Stausosirella* sp. 2
- Pl. 539 *Stenopterobia delicatissima* (Lewis) Van Heurck 1896, morph 2
- Pl. 540 *Stenopterobia delicatissima* (Lewis) Van Heurck 1896, small form
- Pl. 541 *Stephanodiscus medius* Håkansson 1986



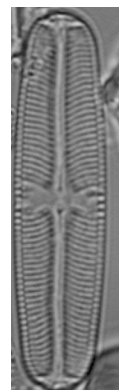
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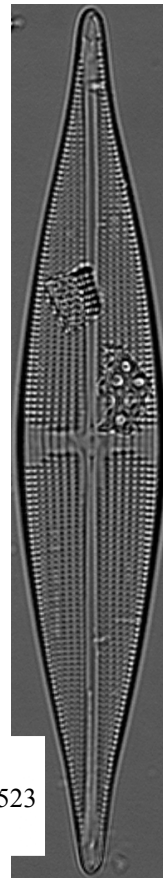
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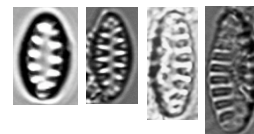
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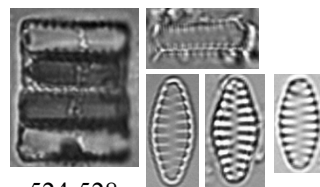
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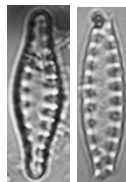
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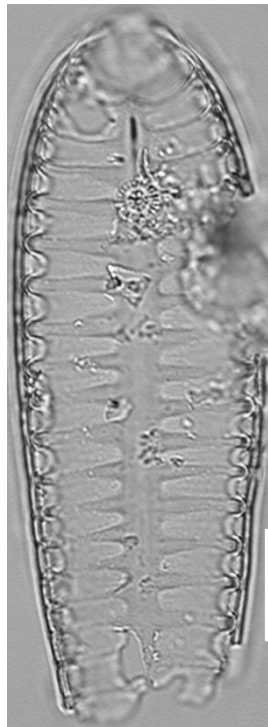
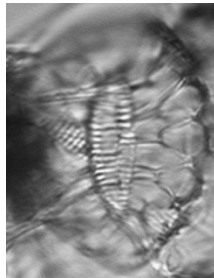
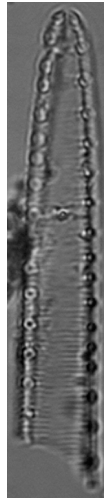
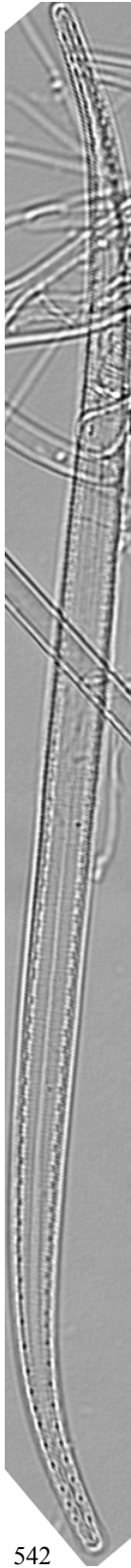


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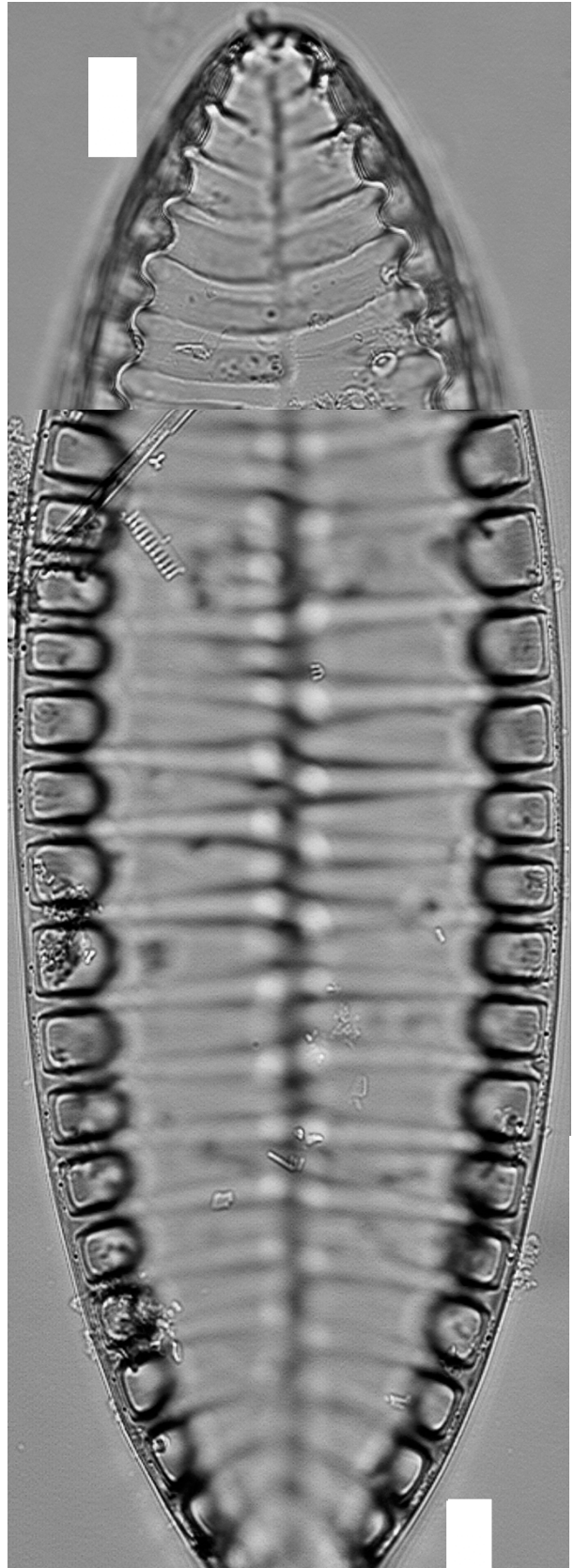


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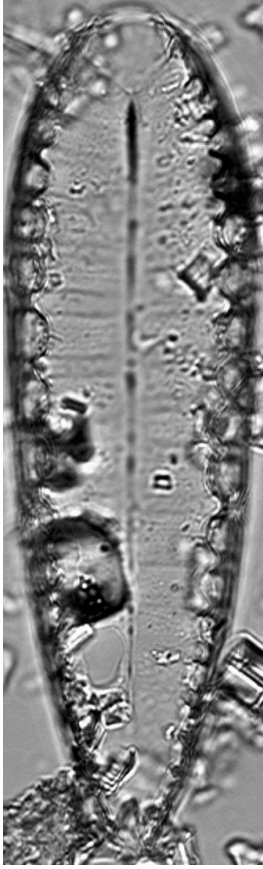
- Pl. 542 *Stenopterobia curvula* (W. Smith) Krammer in Lange-Bertalot & Krammer 1987
(Siver et al. 2005)
- Pl. 543 *Stenopterobia delicatissima* (Lewis) Van Heurck 1896
- Pl. 544 *Stenopterobia delicatissima* (Lewis) Van Heurck 1896, morph 3
- Pl. 545 *Surirella amphioxys* W. Smith 1856
- Pl. 546 *Surirella biseriata* Brébisson in Brébisson & Godey 1836
(Siver et al. 2005)
- Pl. 547 *Surirella tenera* Gregory 1856



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- Pl. 548 *Surirella tenera* Gregory 1856, (continued)
- Pl. 549 *Surirella cuspidata* Hustedt 1942
(Camburn and Charles 2000)
- Pl. 550 *Surirella guatemalensis* Ehrenberg 1854
(Siver et al. 2005)
- Pl. 551 *Surirella linearis* W. Smith 1953
(Siver et al. 2005; Camburn and Charles 2000)
- Pl. 552-554 *Surirella linearis* var. *constricta* Grunow 1862
(Siver et al. 2005; Camburn and Charles 2000)
- Pl. 555 *Fragilariforma spinulosa* (Patrick) Metzeltin & Lange-Bertalot 2007
(Metzeltin and Lange-Bertalot 2007)
- Pl. 556-557 *Tabellaria flocculosa* (Roth) Kützing 1844
(Siver et al. 2005)



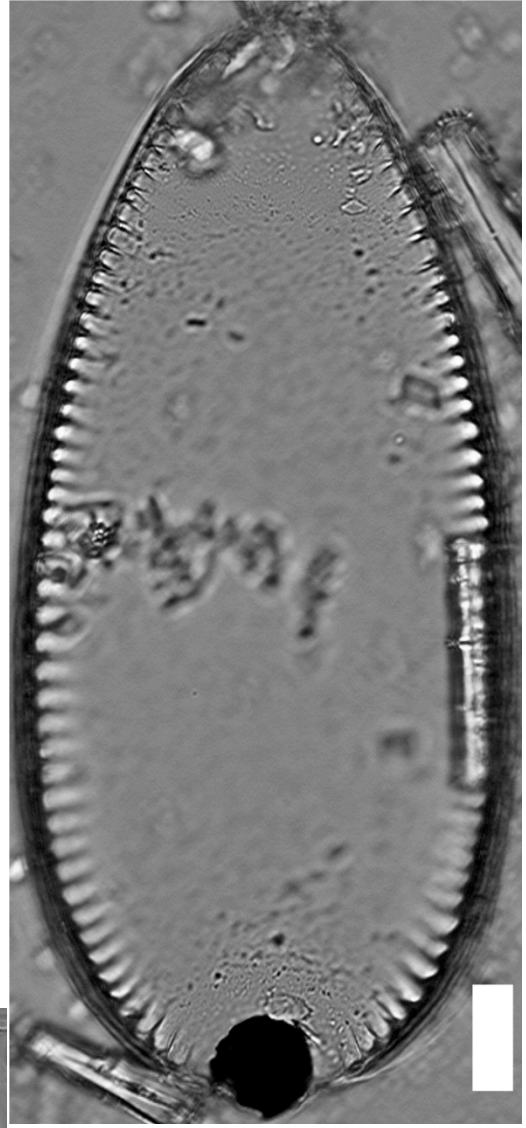
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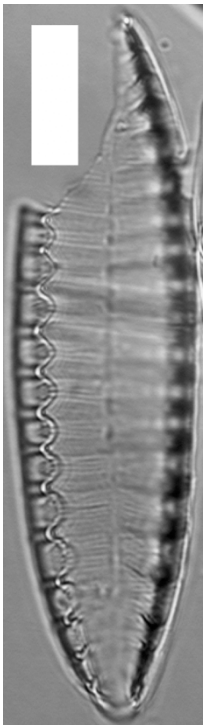
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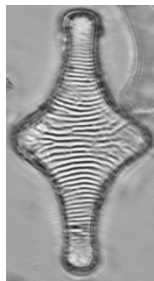
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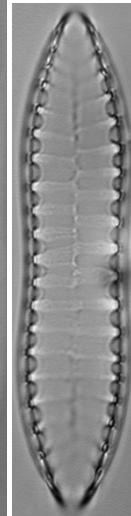
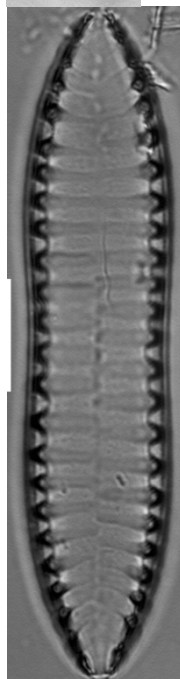
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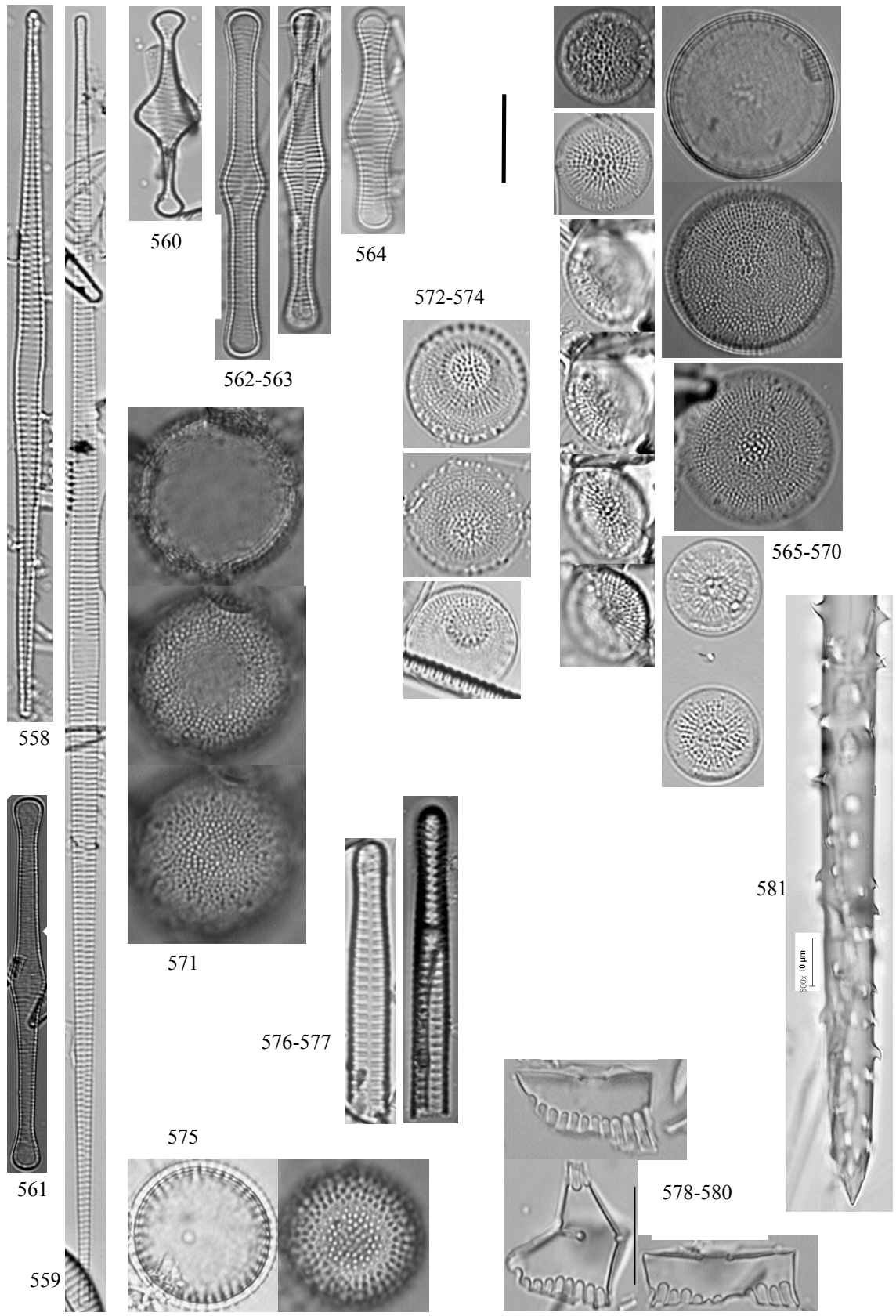
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556-557



- Pl. 558-559 *Synedra acus* var. *angustissima* (Grunow) Van Heurck 1885
(Siver et al. 2005)
- Pl. 560 *Tabellaria flocculosa* (Roth) Kützing 1844, (continued)
(Siver et al. 2005)
- Pl. 561 *Tabellaria flocculosa* var. *linearis* Koppen 1975
(Siver et al. 2005)
- Pl. 562-563 *Tabellaria flocculosa* var. *linearis* Koppen 1975, medium form
- Pl. 564 *Tabellaria flocculosa* var. *linearis* Koppen 1975, small form
- Pl. 565-570 *Thalassiosira rudis* Tremarin, Ludwig, Becker & Torgan sp. nov.
(Ludwig et al. 2008)
- Pl. 571 *Thalassiosira* cf. *rudis* Tremarin, Ludwig, Becker & Torgan sp. nov., auxospore?
- Pl. 572-574 *Thalassiosira* sp. 1
- Pl. 575 *Thalassiosira* sp. 2
- Pl. 576-577 *Ulnaria ulna* (Nitzsch) Compère 2001
(Siver et al. 2005)
- Pl. 578-580 unknown large *Pinnularia*, broken valves
- Pl. 581 Sponge spicule



5 SYNTHESIS

Climate fluctuations result from a combination of natural and human-induced factors. Results from this research offer insight into the future of our changing climate by using as many lines of evidence as possible to draw conclusions about historic hydrologic fluctuations.

The complement of tools supplied in Chapter 2 can be implemented together to provide evidence for diatom-based changes in hydrology from the sediments of Florida sinkhole lakes. Models created from more than one habitat have the advantage that they might be applicable in multiple situations, such as reconstruction of a sediment history from a wetland. Caution is advised, however when applying these models for paleolimnological reconstruction. As seen in Chapter 3, diatoms present in the epiphytes may not have the same experiences with the physico-chemical habitat of a lake as diatoms present in the plankton.

The Lake Annie diatom record from Chapter 3 uncovers both a long-term and recent record of climatic change as well as evidence that anthropogenic activities may have exacerbated the impact of climate change on the lake. The ontogeny of groundwater-connected lakes in the Southeast is unique. It begins with infilling of basin with water to form a wetland. The timing of filling is dependent on the depth of the basin and the level of the water table. Water levels in lakes and wetlands across the Southeast stabilized with climate around 4,000 years ago. Lake Annie is now experiencing another change in water delivery, this time in the context of anthropogenic pressures. Despite the seemingly pristine location, subtle human modifications to the lake and recent climate-driven hydrologic change have combined to shift the lake rapidly into a new paradigm

after nearly 4,000 years of relative stability. Lakes that are not protected, or worse purposefully interfered with, will likely experience climate change even more intensely.

Future Directions

Chapter 2 raises questions about the underlying drivers that might be present in different habitat types. What accounts for the differing responses of plankton and epiphytes to a variable? The integration of a variable's effect on assemblages over time will be different depending on the habitat sampled. While a plankton tow only captures the diatoms alive at that moment, sediments samples contain a combination of assemblages. The availability of periodic physico-chemical data presents the possibility of averaging data over different lengths of time depending on the habitat of interest. It would be interesting to find out the optimum range of data to relate to assemblages from a particular habitat type.

Adding additional samples to the reference set would be desirable after finding in Chapter 3 that the pH reference model did not cover a wide enough range. It would be interesting to research the source of excess TP, higher color, and rising pH in Lake Annie. How much of the change in the lake might be attributable to the man-made ditches, which create artificial overland flow? What changes are present in the groundwater? It would be necessary to find out the properties of the water entering the lake by testing nearby groundwater wells, flowing water in the ditches, and surrounding wetlands.

The presence of the 25-year limnological record and a ^{210}Pb -dated core suggests the possibility of creating a temporal calibration model in addition to the spatial calibration model created in Chapter 2. The advantage is that your model will include

diatoms from Lake Annie related to known levels of measured variables. However, the model would only be applicable over a short time period, as the diatom assemblages have changed drastically since 1970.

One of the most interesting future directions to take this research is to find another lake with an even longer climate history. A 50,000-year pollen record that was recovered from nearby Lake Tulane showed wide fluctuations in plant communities associated with climate (Grimm et al. 1993). It would be interesting to see if the diatom communities alternate in sync with the plant communities given their very different generation times. Diatoms could provide details about the water-delivery regime that cannot be observed in a pollen record.

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