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Gabriela S. Hassan^a

^a Grupo de Ecología y Paleoecología de Ambientes Acuáticos Continentales, Instituto de Investigaciones Marinas y Costeras, CONICET-UNMdP, Mar del Plata, Buenos Aires, Argentina
Mar del Plata, Buenos Aires, Argentina

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Diatom-based reconstruction of Middle to Late Holocene paleoenvironments in Lake Lonkoy, southern Pampas, Argentina

GABRIELA S. HASSAN

Grupo de Ecología y Paleoecología de Ambientes Acuáticos Continentales, Instituto de Investigaciones Marinas y Costeras, CONICET-UNMdP, Mar del Plata, Buenos Aires, Argentina

Diatoms recovered from shallow Lake Lonkoy sediment core in southern Pampas, Argentina, were studied in order to assess past environmental conditions. A total of 47 samples were selected from a 1.42-m long core that spans the last 4840 cal. years. Diatoms were extracted by chemical cleaning and studied under light and scanning electron microscopy. A total of 89 diatom taxa were recorded, including 36 taxa that reached > 2% relative abundance and were used in statistical analyses. A cluster analysis allowed five significant diatom association zones (DAZ) to be defined. DAZ I (142–92 cm) was dominated by *Cyclotella meneghiniana* Kützing, *Cocconeis placentula* Ehrenberg and *Nitzschia hustedtiana* Salah, and a low abundance of aerophilic taxa, indicating brackish water conditions probably related to the Holocene sea-level high stand. DAZ II (90–48.5 cm) was dominated by *C. meneghiniana* and *Aulacoseira granulata* (Ehrenberg) Simonsen, representing a period of high nutrient loading and turbid conditions in the lake, associated with higher water levels and lower salinities than the environmental conditions in DAZ I. The upper 50 cm of the core (DAZ III to V) showed an increase in the dominance of brackish epiphytic and hypereutrophic benthic taxa, indicating an increase in nutrient concentrations associated with agricultural human impacts in the basin. Overall, diatoms allowed major paleoenvironmental changes to be inferred for the lake during the Holocene.

Keywords: *shallow lake, paleoecology, Holocene, southern Pampas, Argentina*

Introduction

Diatoms are powerful and reliable paleoenvironmental indicators, mainly as a consequence of their durability, the high preservation potential of their siliceous frustules, high abundance and diversity, and differences in species responses to environmental conditions (Battarbee 1986, Battarbee et al. 2001, Julius & Theriot 2010). In freshwater environments, they have played a major role in the reconstruction of past climate changes, being used as proxy indicators to reconstruct Holocene climate variability on every continent (e.g., Kilham et al. 1996, Gasse et al. 1997, Smol & Cumming 2000, Mackay et al. 2003).

Most diatom-based paleoclimatic records come from North America and Europe, while the number of studies in South America is considerably lower (e.g., González & Maidana 1998, Jenny et al. 2002, Markgraf et al. 2003, Tapia et al. 2003, Moro et al. 2004, Fey et al. 2009). Hence, many questions regarding the natural climatic cycles and the strength of human-induced changes remain unanswered for vast regions of South America (Villalba et al. 2009). This is the case for the Pampa plain, an area in which the prevailing flat geomorphology promotes the occurrence of numerous shallow lakes that contain archives of Holocene environmental changes (García-Rodríguez et al. 2009). Most of these water bodies are small and shallow (< 500 ha in

surface area and up to c. 4 m deep), and characterized by conductivity ranging from oligo- to hyperhaline, naturally high nutrient concentrations, and dense and rich macrophyte communities (Giorgi et al. 2005). Their dynamics are intricately linked to climatic conditions and anthropogenic activities (Fernández Cirelli & Miretzky 2004), as is evident from the pronounced hydrological variability that characterized these water bodies during the twentieth century (e.g., lake-level fluctuations, varying river discharges, extension of flooded lowlands, see García-Rodríguez et al. 2009). Despite their abundance and climatic sensitivity, only one Holocene paleoenvironmental change study has used diatom analysis on these systems (Stutz et al. 2010).

Recently, a series of studies performed in shallow lakes from southern Pampas provided Holocene paleoenvironmental reconstructions based on pollen, non-pollen palynomorphs and plant macroremains (Stutz et al. 2010, 2012). The diatom assemblages preserved in one of these cores from Lake Lonkoy are presented here (Stutz et al. 2012). The main objective of this study is to assess the Holocene paleoclimatic and paleoenvironmental changes that occurred on the southern Pampa plain using diatom analysis. The results are compared with those obtained by Stutz et al. (2010, 2012) and are discussed in a paleolimnological context.

*E-mail: g Hassan@conicet.gov.ar

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Material and methods

Field and laboratory methods

In April 2009, a sediment core was recovered from the center of the small (200 ha) and shallow (< 1.5 m deep) Lake Lonkoy (37°37'S, 57°25'W) in the southeastern Pampa plain, Argentina, using a modified Livingston corer (Fig. 1). The lake was sampled during a dry (La Niña) year and consequently was completely dry. The chronology of the core was determined using accelerator mass spectrometry radiocarbon dating (Stutz et al. 2012). Seven dates were obtained on *Heleobia parchappii* gastropod shells (Table 1) and three lithological units were recognized (Stutz et al. 2012). The lowermost sediment core (142–75 cm) consisted of clayey silt with abundant mollusk shells and low organic matter content (< 10%), which increased slightly towards the top of the unit. From 75 to 15 cm depth, the core consisted of

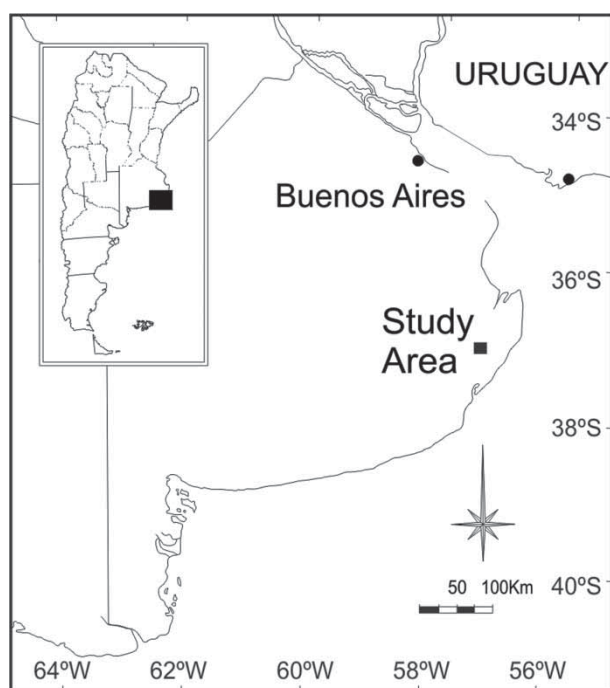


Fig. 1. Location of the study area in Lake Lonkoy, southern Pampas, Argentina.

sandy silt, with organic matter increasing gradually up to 40% at 30 cm depth. The topmost 15 cm were characterized by black silty sediments and the highest percentage of organic matter (80%). In the laboratory, the core was sectioned at contiguous 1-cm intervals. A total of 47 samples were selected for diatom analysis.

In the laboratory, samples were oxidized with 30% hydrogen peroxide and 10% hydrochloric acid, washed several times with distilled water and diluted to a total volume of 100 mL. After complete homogenization, a subsample was transferred to a coverslip and air-dried, and permanent slides were made using Naphrax®. On each slide, at least 300 diatom valves were counted across random transects using a Leica DM500 light microscope (LM) at $\times 1000$ magnification. Light micrographs were taken using a Leica ICC50 digital camera. For scanning electron microscopy (SEM), cleaned material was mounted on 3- μm pore polytungstate membrane filters, sputter-coated with 12 nm gold using a Denton Vacuum Desk II evaporator (Denton Vacuum LLC, Moorestown, NJ, USA) and examined using a Jeol JSM6460LV SEM (JEOL Ltd, Tokyo, Japan) operating at 15 kV. Diatom taxa were identified according to Lange-Bertalot et al. (1996), Krammer & Lange-Bertalot (1997, 1999, 2004a, b), Metzeltin & Lange-Bertalot (1998, 2007), Rumrich et al. (2000), Metzeltin et al. (2005), Levkov (2009) and Sar et al. (2009). Diatom taxa were characterized according to their salinity tolerances and life form following the ecological classifications by Vos & de Wolf (1993), Van Dam et al. (1994), and modern data available for the pampas region (Izaguirre & Vinocur 1994a, b, Hassan et al. 2009, 2011).

Data analyses

Diatom relative abundance data were square root transformed prior to statistical analyses in order to stabilize their variances (Bigler et al. 2006). Only taxa with > 2% relative abundance in at least one sample were used in data analyses. Diatom zones in the fossil sequences were defined using constrained hierarchical clustering based on Bray–Curtis distance matrices, with clusters constrained

Table 1. Accelerator mass spectrometry radiocarbon dates from Lake Lonkoy. All dates were performed on shells of the gastropod *Heleobia parchappii*.

Sample depth (cm)	^{14}C age BP	Cal. yrBP (2 σ range)	Laboratory no.	Source
47–48	247 \pm 21	200 (151–308)	UBA20715	This work
79–80	770 \pm 35	670 (570–730)	AA87091	Stutz et al. (2012)
89–90	1310 \pm 35	1200 (1080–1280)	AA89347	Stutz et al. (2012)
100–101	1830 \pm 35	1700 (1600–1820)	AA92536	Stutz et al. (2012)
110–111	2300 \pm 35	2240 (2150–2280)	AA92537	Stutz et al. (2012)
120–121	3540 \pm 40	3760 (3640–3870)	AA89348	Stutz et al. (2012)
142–143	4325 \pm 40	4840 (4650–4970)	AA87092	Stutz et al. (2012)

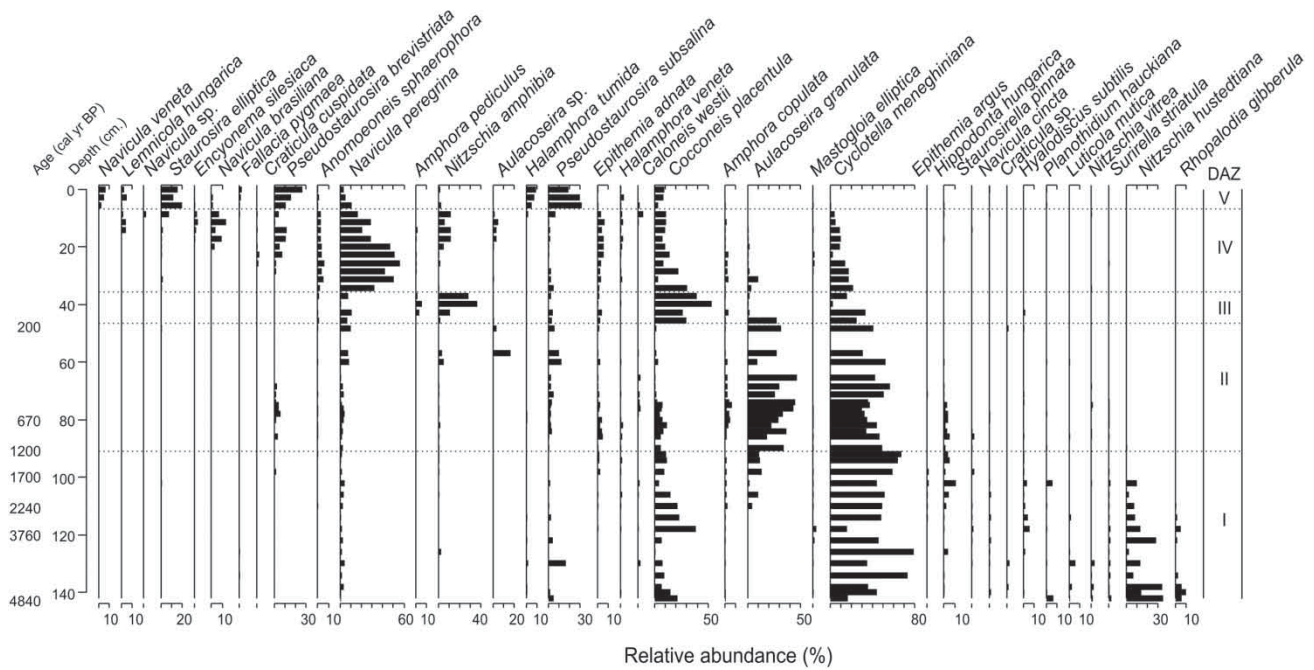


Fig. 2. Relative abundance of the dominant diatom taxa in the Lake Lonkoy sediment core, with diatom association zones (DAZ I to V) obtained from cluster analysis (see text) and seven radiocarbon dates (see text and Stutz et al. 2012).

by stratigraphic order. The statistical significance of the diatom zones was assessed using the ‘broken stick’ model (Bennett 1996).

A detrended correspondence analysis (DCA) was used to summarize the multivariate data (Hill & Gauch 1980). This analysis allows multivariate paleolimnological data sets to be presented as low-dimensional plots of sample points on the principal axes 1 and 2, and as stratigraphical plots of major ordination axis sample scores. The ‘composite curves’ are based on many taxa that contribute to the major axes of variation or underlying latent structure in the total data, thus providing a useful summary of the major patterns of variation within the data (Birks 2012). Changes in the sample scores on the major ordination axes are used to interpret the gradual and often complex transitions from one assemblage to another and to assess results of zonation techniques. DCA calculates the length of the species gradients (DCA axis 1 scores), which describe the degree of species turnover. A 50% change in species composition occurs at c. 1.0–1.4 standard deviation (SD) units and gradient lengths more than 4 SD indicate a complete turnover of species (Heino & Soinenen 2005).

All analyses and graphs were made using the software R version 2.12.2 (R Development Core Team 2011), including the packages ‘vegan’ version 1.17–8 (Oksanen et al. 2011) and ‘rioja’ version 0.5–6 (Juggins 2009).

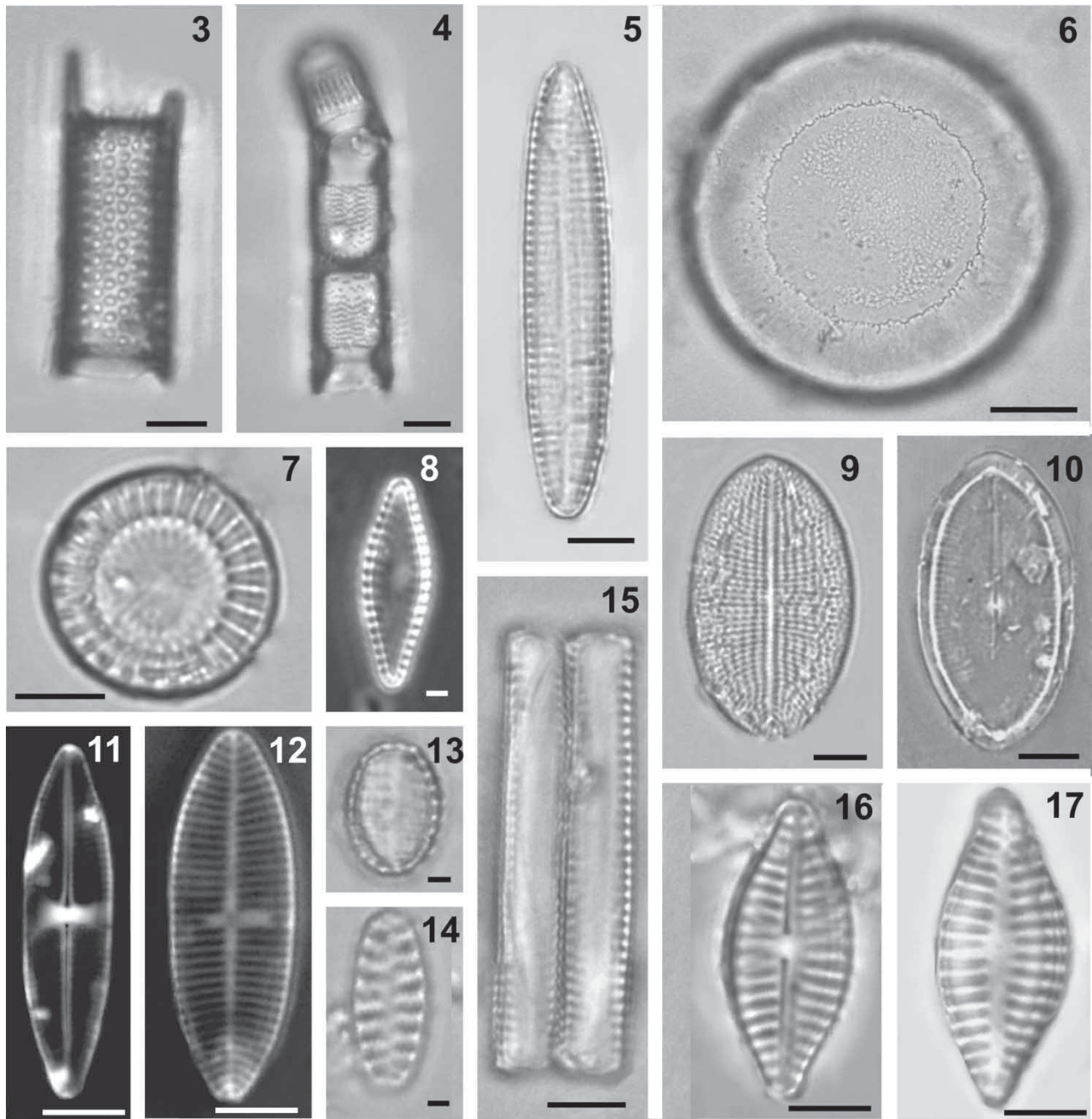
Results

A total of 81 diatom taxa were identified along the Lonkoy sequence (Fig. 2). Light and scanning electron

microphotographs of dominant taxa are presented in Figs 3–51. Only 36 of these taxa reached > 2% relative abundance and were used in the cluster analysis. Results of the cluster analysis (Fig. 2) allowed five significant diatom association zones (DAZI to V) to be defined.

DAZI (142–92 cm) was dominated by *Cyclotella meneghiniana* Kützing, *Cocconeis placentula* Ehrenberg and *Nitzschia hustediana* Salah (Fig. 2), accompanied by low abundance of *Hippodonta hungarica* (Grunow) Lange-Bertalot, Metzeltin & Witkowski, *Hyalodiscus subtilis* Bailey and *Surirella striatula* Turpin. This zone was characterized by the dominance of brackish/freshwater plankton intercalated with peaks of brackish benthos and aerophilic taxa (Fig. 52). Samples from DAZI formed a defined cluster in the DCA ordination plot, showing low compositional variability. DCA axis 1 scores were very stable, ranging between -0.5 and -1, indicating a stable specific composition of the diatom assemblages along the main axis of the variation (Fig. 53). However, the variability in DCA axis 2 scores was larger (0 to -1.5).

DAZ II (90–48.5 cm) was also dominated by *C. meneghiniana*, but with an increase in the abundance of *Aulacoseira granulata* (Ehrenberg) Simonsen (Fig. 2). According to their ecological characteristics, this diatom assemblage is composed mainly of freshwater/brackish (salinity of 0.2–0.9) and brackish/freshwater (salinity of 0.9–1.8) planktonic taxa (Fig. 52). From the DCA analysis, there was no significant turnover of taxa in this zone or among DAZ I and DAZ II. These two zones formed discrete clusters in the ordination plot, separated mainly by DCA axis 2 scores

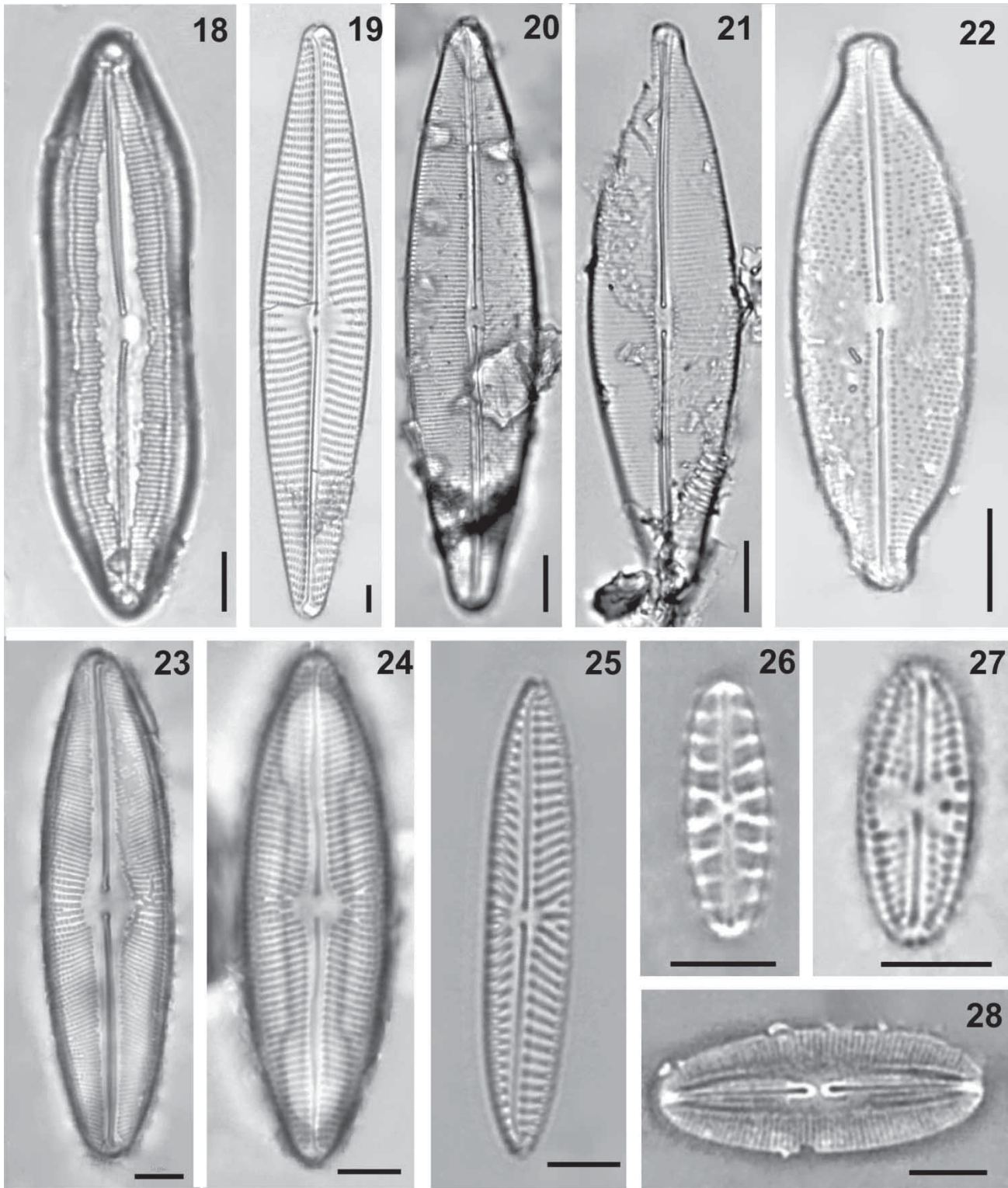


Figs 3–17. Dominant diatom taxa from Lake Lonkoy sediment core, LM. **Fig. 3.** *Aulacoseira granulata*. **Fig. 4.** *Aulacoseira* sp. **Figs 5, 15.** *Pseudostaurosira subsalina* in valve and girdle views, respectively. **Fig. 6.** *Hyalodiscus subtilis*. **Fig. 7.** *Cyclotella meneghiniana*. **Fig. 8.** *Pseudostaurosira brevistriata*. **Fig. 9.** *Cocconeis placentula*, raphe valve. **Fig. 10.** *Cocconeis placentula*, rapheless valve. **Fig. 11.** *Lemnicola hungarica*, raphe valve. **Fig. 12.** *Lemnicola hungarica*, rapheless valve. **Fig. 13.** *Staurosira elliptica*. **Fig. 14.** *Staurosirella pinnata*. **Fig. 16.** *Planothidium hauckiana*, raphe valve. **Fig. 17.** *Planothidium hauckiana*, rapheless valve. Scale bars = 5 μm (Figs 3–7, 9–12, 15–17); 1 μm (Figs 8, 13–14).

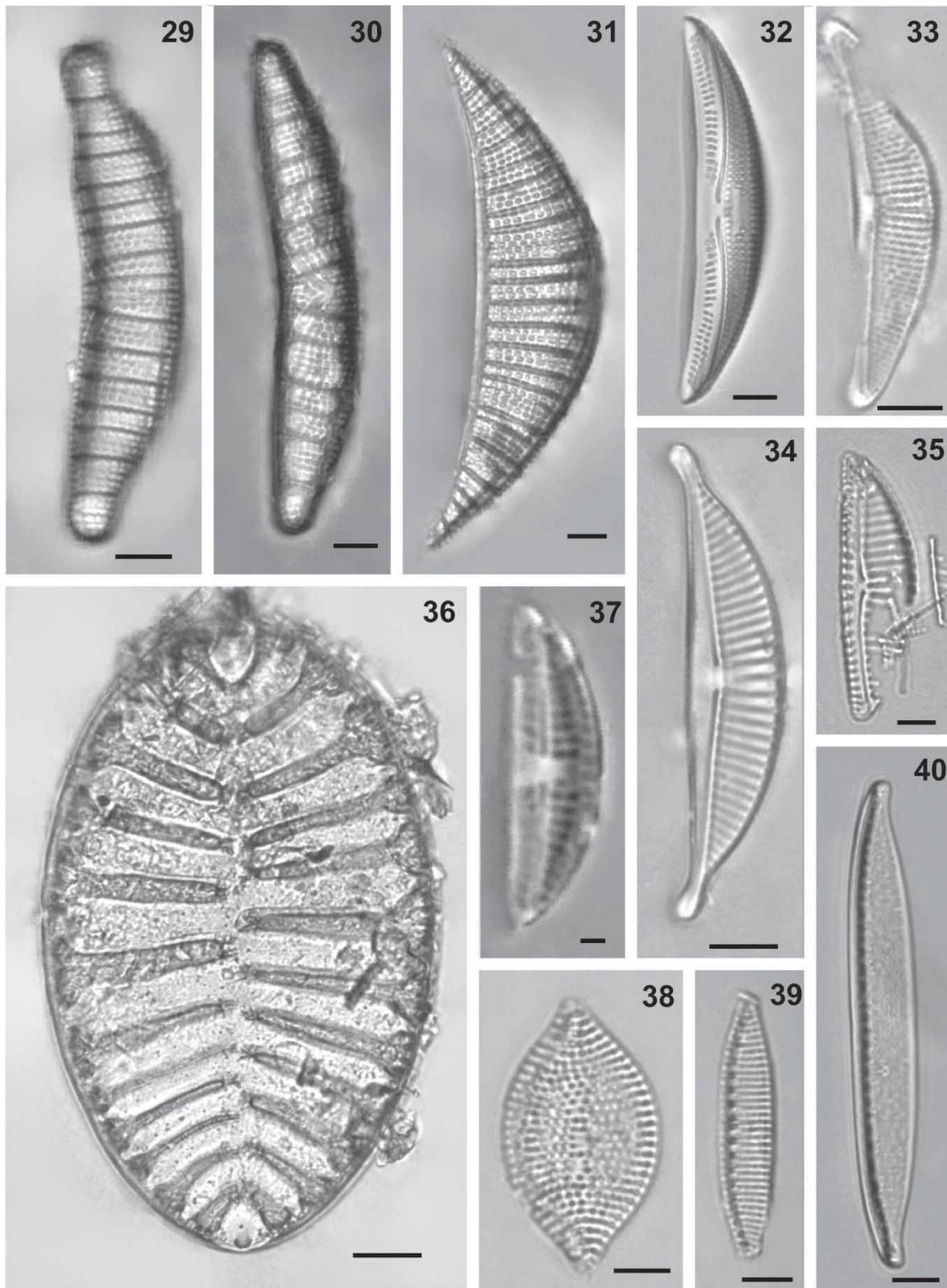
(Fig. 53). Again, the differences between these zones are given by shifts in the relative abundance of the dominant taxa rather than by the changes in the specific composition of the assemblages.

DAZ III (45.5–37 cm) was characterized by an increase in the abundance of *C. placentula*, accompanied by the

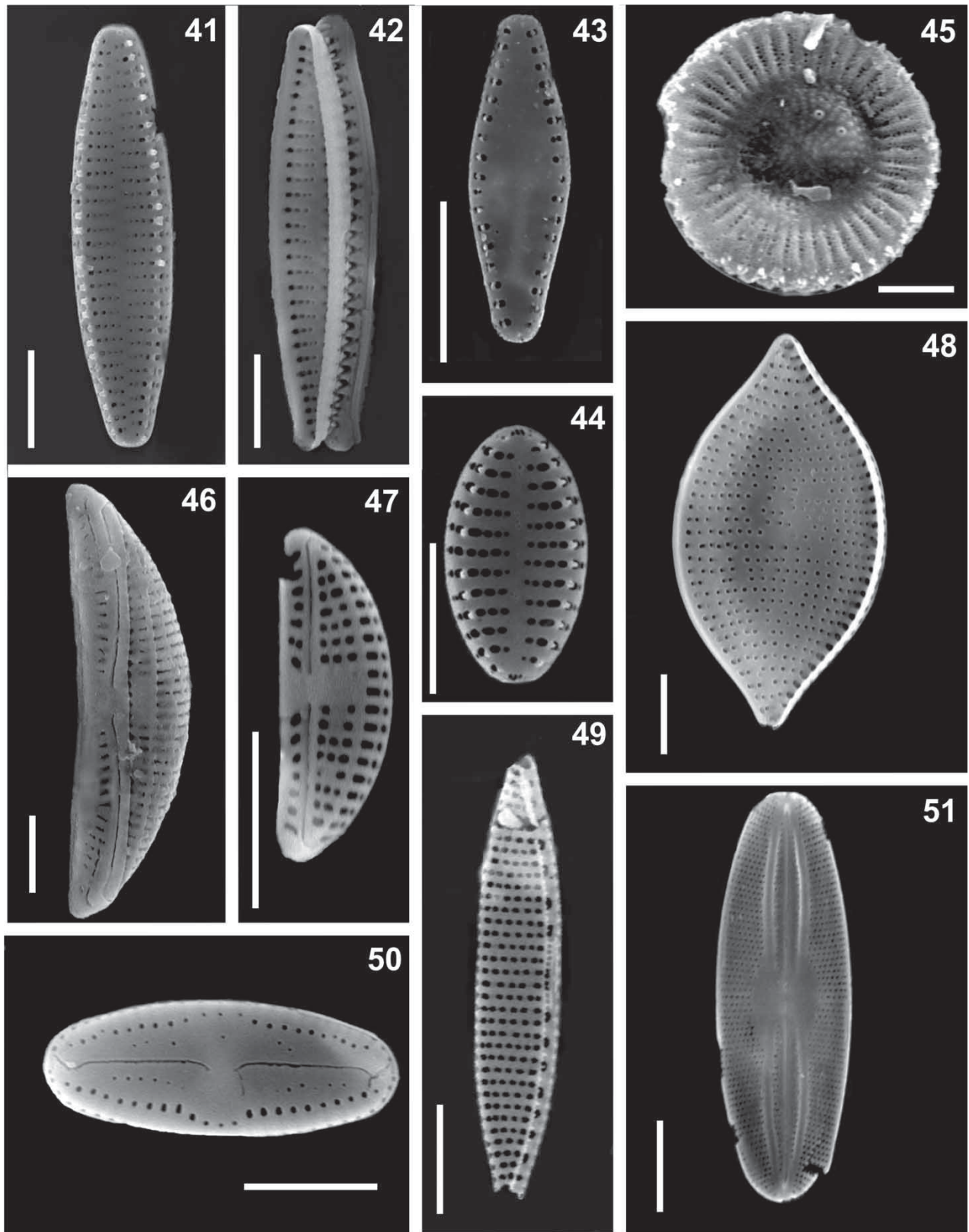
hypereutrophic *Nitzschia amphibia* Grunow and low abundance of *C. meneghiniana* (Fig. 2). According to their ecological preferences, the diatom assemblage in this zone is dominated by epiphytic taxa of freshwater/brackish water preference (Fig. 52). DCA shows an abrupt species turnover in this zone, with DCA axis 1 scores showing an increasing



Figs 18–28. Dominant diatom taxa from Lake Lonkoy sediment core, LM. **Fig. 18.** *Caloneis westii*. **Fig. 19.** *Navicula peregrina*. **Fig. 20.** *Craticula* sp. **Fig. 21.** *Craticula cuspidata*. **Fig. 22.** *Anomooneis sphaerophora*. **Fig. 23.** *Navicula brasiliana* var. *platensis*. **Fig. 24.** *Mastogloia elliptica*. **Fig. 25.** *Navicula cincta*. **Fig. 26.** *Hippodonta hungarica*. **Fig. 27.** *Luticola mutica*. **Fig. 28.** *Fallacia pygmaea*. Scale bars = 10 μm (Figs 18–22); 5 μm (Figs 23–28).



Figs 29–40. Dominant diatom taxa from Lake Lonkoy sediment core, LM. **Fig. 29.** *Epithemia adnata*. **Fig. 30.** *Epithemia argus*. **Fig. 31.** *Rhopalodia gibberula*. **Fig. 32.** *Amphora copulata*. **Fig. 33.** *Halamphora veneta*. **Fig. 34.** *Halamphora tumida*. **Fig. 35.** *Encyonema silesiacum*. **Fig. 36.** *Surirella striatula*. **Fig. 37.** *Amphora pediculus*. **Fig. 38.** *Nitzschia hustedtiana*. **Fig. 39.** *Nitzschia amphibia*. **Fig. 40.** *Nitzschia vitrea*. Scale bars = 20 μm (Fig. 36); 5 μm (Figs 29–35, 38–40); 1 μm (Fig. 37).



Figs 41–51. Selected diatom taxa from Lake Lonkoy sediment core, SEM external (Figs 41, 43–47, 52–53) and internal (Figs 42, 48, 51) views. **Figs 41–42.** *Pseudostaurosira subsalina*. **Fig. 43.** *Pseudostaurosira brevistriata*. **Fig. 44.** *Staurosira elliptica*. **Fig. 45.** *Cyclotella meneghiniana*. **Fig. 46.** *Amphora copulata*. **Fig. 47.** *Amphora pediculus*. **Fig. 48.** *Nitzschia hustediana*. **Fig. 49.** *Nitzschia amphibia*. **Fig. 50.** *Luticola mutica*. **Fig. 51.** *Fallacia pygmaea*. Scale bars = 5 μm .

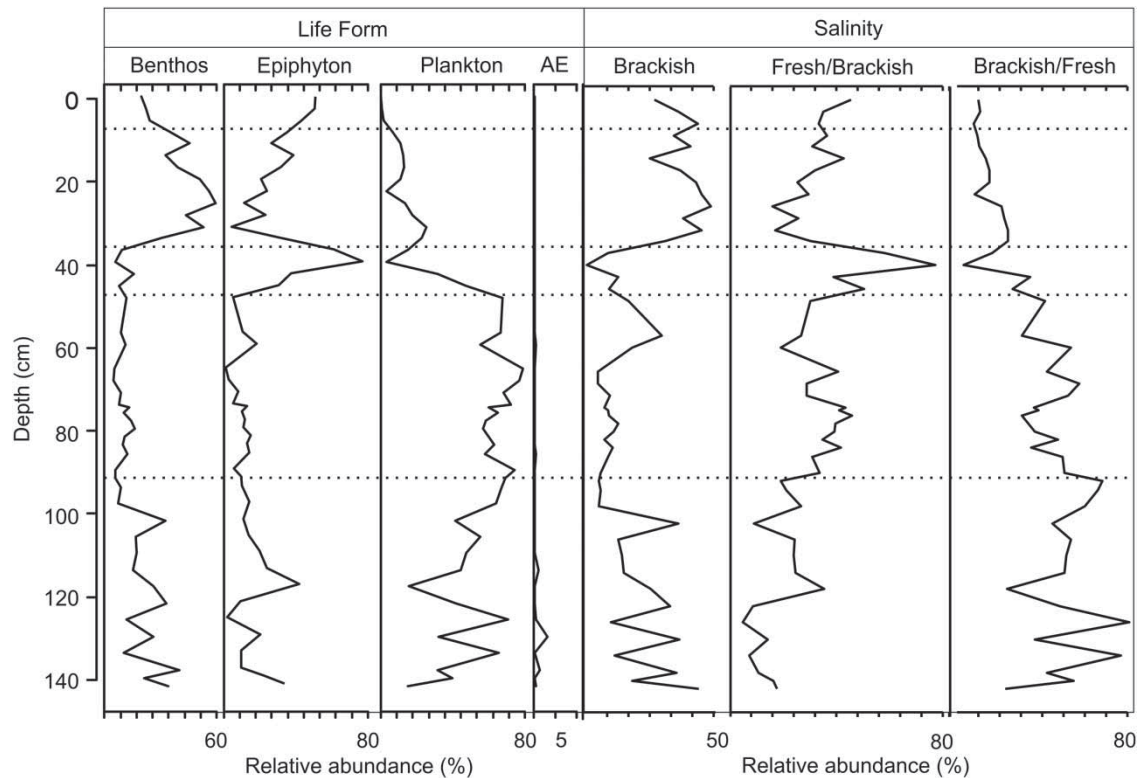


Fig 52. Distribution of the relative abundance (%) of the main life form and salinity groups of diatom taxa along the Lake Lonkoy sediment core. AE: aerophilic taxa. Dotted lines indicate the diatom zones defined by cluster analysis based on taxa relative abundances (see Fig. 2).

trend and reaching positive values at the top of the zone (Fig. 53). Samples of this zone were ordered separately from those of DAZ I and DAZ II in the DCA ordination plot, probably as a consequence of the decrease in the relative abundance of *C. meneghiniana* and the increase in the proportion of epiphytic taxa (Fig. 52).

DAZIV (34–8 cm) was characterized by a high abundance of *Navicula peregrina* (Ehrenberg) Kützing, a robust diatom characteristic of shallow brackish waters, accompanied by low abundance of *C. meneghiniana*, *C. placentula*, *N. amphibia*, *Epithemia adnata* (Kützing) Brébisson, *Pseudostaurosira brevistriata* (Grunow) Williams & Round and *Navicula brasiliensis* var. *platensis* Frenguelli (Fig. 2). Overall, this zone was dominated by benthic taxa of brackish water preference, accompanied by a low proportion of epiphytic taxa (Fig. 52). DCA shows that the tendency for species turnover that characterized DAZ III continues towards the top of DAZ IV (Fig. 53).

DAZ V (6–0 cm) was dominated by benthic and epiphytic taxa, such as *Pseudostaurosira subsalina* (Hustedt) Morales, *P. brevistriata*, *Staurosira elliptica* (Schumann) Williams & Round, *Halamphora tumida* (Hustedt) Levkov, *Navicula veneta* Kützing and *Lemnicola hungarica* (Grunow) Round & Basson (Fig. 2). According to the DCA, the specific composition of the assemblages reached their highest turnover values in this zone, which represents the culmination of a change initiated at the top of DAZ II; a

total difference of c. 2.5 SD occurred in the top 60 cm of the core (Fig. 53).

Discussion

The fluctuations in the relative abundances of diatom taxa and the changes in specific composition of the assemblages preserved in Lake Lonkoy indicate clear paleoenvironmental changes that occurred during the Middle and Late Holocene. According to the cluster analysis of the diatom assemblages, it was possible to identify five different zones in the evolution of the lake.

The first zone, DAZ I, clustered samples span c. 3500 years of lake history, between c. 4800 and 1200 cal. yr BP (Stutz et al. 2012). The zone is dominated by *C. meneghiniana*, a planktonic euryhaline species that can be found in a variety of habitats, ranging from freshwater to marine conditions (Tuchman et al. 1984, Håkansson & Chepurnov 1999, Roubex & Lancelot 2008). This is one of the most widely distributed species in the modern diatom flora of the pampean shallow lakes, where it dominates under alkaline (pH 8–10.5), slightly brackish (1–7 mS·cm⁻¹) and eutrophic to hypereutrophic conditions (Vouilloud 2003, Hassan et al. 2009, 2011). Nevertheless, it is also found in lakes with low phosphate (PO₄³⁻) concentrations (between 0 and 430 mg L⁻¹, Hassan et al. 2011). The species is also common in estuaries of the

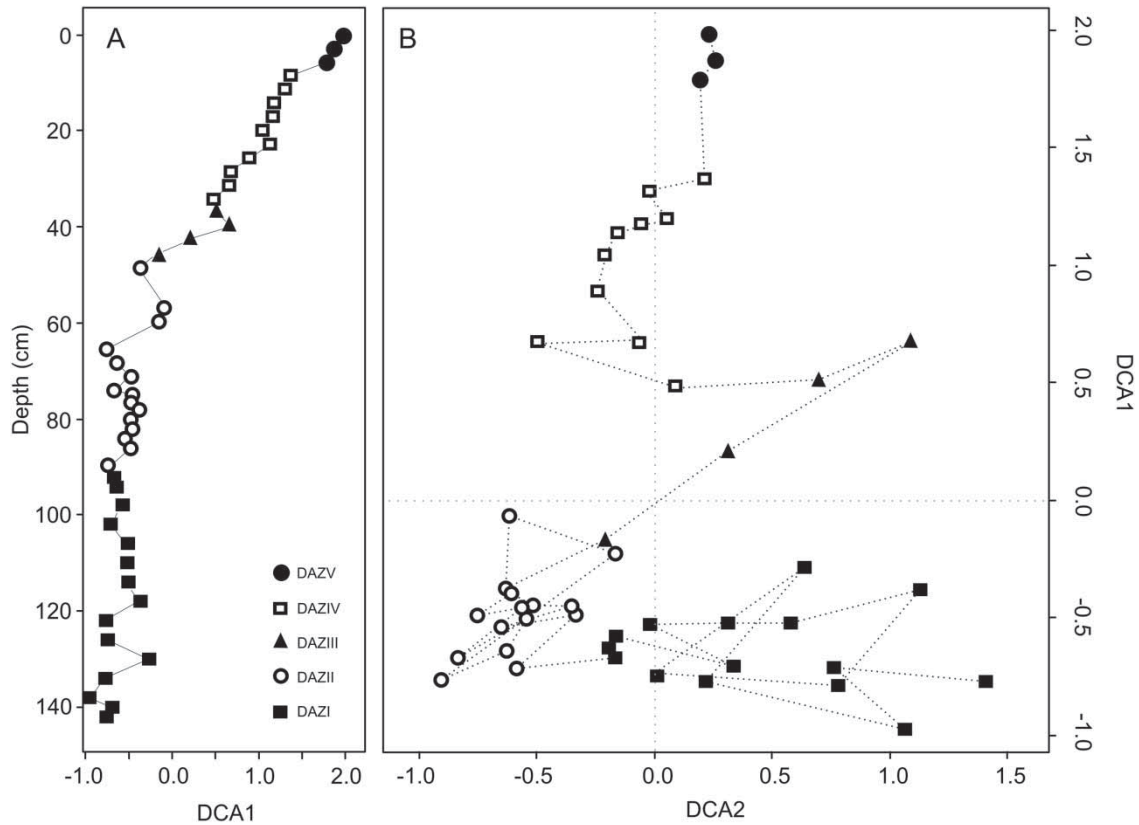


Fig 53. (A) Plot of DCA axis 1 scores along the Lake Lonkoy DAZ zones and (B) DCA ordination plot of Lake Lonkoy samples. Showing shifts in species composition through time. Symbols indicate the different diatom zones (DAZ I–V) defined by cluster analysis and presented in Figure 2.

region and a salinity optimum of 6.3 ± 7.5 for this species was calculated by weighted averaging methods (Hassan et al. 2009). The fluctuations in abundance of *C. meneghiniana*, together with the co-occurring salt-tolerant and non-planktonics *C. placentula* and *N. hustediana* and occasional presence of brackish *H. subtilis* indicate periods of high water conductivity (Frenguelli 1945, Bracco et al. 2005).

The brackish affinity of DAZ I dominant taxa may suggest marine influences in the basin during the Middle Holocene. The proposed sea level was then c. 2 m above the modern level (Isla & Espinosa 1998), which may have elevated the water table and induced groundwater salinization in the southern Pampas region. Hence, ingress of groundwater marine brines into the lake is likely responsible for the high conductivity inferred for this period. Similarly, Stutz et al. (2002, 2006, 2010) inferred brackish conditions dominating two other pampean lakes, Nahuel Rucá and Hinojales, during the Middle Holocene and interpreted these as seawater intrusion during the last sea-level high stand; these two lakes are compared with Lake Lonkoy in Fig. 54. Pollen and non-pollen palynomorph data from Lake Lonkoy also suggest brackish to saline conditions in the lake during this period (Stutz et al. 2012; Fig. 54). Moreover, diatom assemblages in Lake Nahuel Rucá are

also dominated by saline taxa, such as *Campylodiscus clypeus* (Ehrenberg) Ehrenberg, *S. striatula* and *Caloneis formosa* (Gregory) Cleve, suggesting environmental conditions similar to Lake Lonkoy (Fig. 54). However, Lake Lonkoy is situated further inland (Fig. 1) and the possibility that surface seawater directly affected the lake seems unlikely. As well as groundwater changes, it is possible that higher evaporation–precipitation ratios prevailed during the Middle–Late Holocene in the Pampa plain as a consequence of the eastward displacement of the arid–semiarid region (Mancini et al. 2005, Stutz et al. 2012). The absence of truly marine planktonic diatom taxa, such as *Actinocyclus* spp. or *Paralia sulcata* (Ehrenberg) Cleve, which have been indicated as stratigraphic indicators of transgressive processes in the pampean coast (Espinosa & Isla 2011, Hassan et al. 2011), also argues against a direct effect of marine tides into the Lonkoy basin. Therefore, the combination of an increased input of brackish groundwater and evaporation is suggested as an explanation for lake permanency and its salinization during the Middle Holocene.

DAZ II was also dominated by *C. meneghiniana*, but with the co-dominance of *A. granulata*. The latter is a freshwater/brackish planktonic taxon indicative of high nutrient concentrations and low light availability, common

Lake Lonkoy		Lake Nahuel Rucá
Pollen and non-pollen palynomorphs	Diatoms	
<p>0 – 200 cal yr BP: Onset of the modern lake conditions. Diverse emergent macrophytes (<i>Schoenoplectus californicus</i>, <i>Bacopa monnieri</i>, <i>Alternanthera philloxeroides</i>, <i>Ranunculus apiifolius</i>, <i>Polygonum punctatum</i>, <i>Phyla canescens</i>, <i>Triglochin striata</i>, <i>Hydrocotyle bonariensis</i> and <i>H. ranunculoides</i>) growing as a belt, where a carpet of free-floating plant species (<i>Lemna valdiviana</i>, <i>Wolffiella lingulata</i>, <i>Azolla filiculoides</i> and <i>Ricciocarpus natans</i>) develops.</p> <p>670 – 200 cal yr BP: Well established freshwater system. High values of <i>Pediastrum</i> and <i>Scenedesmus</i> indicate a shift to a turbid state, which would have decreased light conditions producing loss of submerged macrophytes. Higher primary productivity sustain larger populations of Cladocera, bryozoans and other invertebrates that feed on algae and detritus.</p> <p>4840 – 670 cal yr BP: Dominance of <i>Peridinium</i> and <i>Cobricosphaeridium</i> and the highest pollen percentages of <i>Ruppia</i> indicate brackish to saline conditions. Short-periodic pulses of freshwater are suggested by the presence of <i>Myriophyllum</i>, planktonic algae and Zygnemataceae. The abundance of Charophytes indicates a clear lake and/or low water levels and also brackish to saline conditions.</p>	<p>0 – 200 cal yr BP: Dominance of periphytic and benthic diatoms (<i>Navicula peregrina</i>, <i>Cocconeis placentula</i>, <i>Nitzschia amphibia</i>, <i>Pseudostaurosira subsalina</i>, <i>P. brevistriata</i>, <i>Staurosira elliptica</i> and <i>Navicula brasiliana</i> var. <i>platensis</i>). Hypereutrophic taxa suggest increase of nutrient loadings and inorganic turbidity, probably associated to intensive farming activities in the basin.</p> <p>1200 – 200 cal yr BP: Dominance of <i>Aulacoseira granulata</i> and <i>Cyclotella meneghiniana</i>, indicating eutrophic, organic-turbid and freshwater conditions.</p> <p>4840 – 1200 cal yr BP: Dominance of brackish diatoms (<i>Nitzschia hustediana</i>, <i>Cyclotella meneghiniana</i>, <i>Cocconeis placentula</i>, <i>Hyalodiscus subtilis</i>) indicate brackish to saline conditions, possibly related to increased marine influence related to the Holocene sea-level highstand.</p>	<p>Uppermost 20 cm: Increase in epiphytic brackish/freshwater diatoms suggests an increase in salinity, probably related to periodic droughts. Pollen and plant macrofossils indicate a shallow, freshwater lake similar to present.</p> <p>740 cal yr BP – ? (20 cm) : Maximum values of <i>Aulacoseira granulata</i>, <i>Cyclotella meneghiniana</i> and <i>Aulacoseira muzzaensis</i>, indicating turbid and freshwater conditions. The relationship between submersed macrophytes (<i>Myriophyllum</i>, <i>Potamogeton</i>, <i>Ceratophyllum</i>, <i>Chara</i>) and planktonic algae (Chlorophyta and diatoms), suggests a shift in the lake from a clear to a turbid state.</p> <p>3680 – 740 cal yr BP: Highest values of <i>Campilodiscus clypeus</i>, <i>Surirella striatula</i> and <i>Caloneis formosa</i>, brackish ostracods, and presence of foraminifera indicate brackish to saline conditions. Pollen and plant macrofossils of the submersed macrophytes <i>Myriophyllum</i>, <i>Potamogeton</i>, <i>Ceratophyllum</i> and <i>Chara</i> suggest a clear water body with considerable light penetration.</p> <p>Prior to 3680 cal yr BP: No diatoms. Pollen, dinoflagellate cysts and ostracods suggested brackish/saline conditions in the lake and nearby areas, probably related to sea water intrusion.</p>

Fig 54. Comparison of the environmental history between Lake Lonkoy and Lake Nahuel Rucá based on pollen, non-pollen palynomorphs (Stutz et al. 2012) and diatom analyses (information for Lake Nahuel Rucá from Stutz et al. 2010).

in a wide variety of shallow and well-mixed aquatic systems (Kilham & Kilham 1975, Anderson 2000, Fritz et al. 2012). It has heavy silicified cells with a high sinking rate, and requires turbulence to maintain its presence in the water column (Bradbury 1975). Increasing turbulence (sometimes corresponding to nutrient increases) in a lake can favor this genus over other planktonic species (Dong et al. 2008). *Aulacoseira granulata* and its varieties are widely distributed in the pampean region (see references in Vouilloud 2003), being common in turbid and eutrophic shallow lakes (e.g., Izaguirre & Vinocur 1994a, b, Gómez 1995, Gabellone et al. 2001, Hassan et al. 2011, G.S. Hassan, unpubl. data). A similar diatom assemblage, almost exclusively composed of *C. meneghiniana* and *A. granulata*, was recorded in Lake San Antonio, an alkaline (pH 9.4), freshwater/brackish (conductivity = 4 mS cm⁻¹) and eutrophic (430 mg PO₄³⁻ L⁻¹) turbid shallow lake, with low macrophyte development (Hassan et al.

2011). Hence, DAZ II represents a period of higher nutrient loadings and turbid conditions, and lower salinities than DAZ I. This change in the limnological conditions occurred c. 1000 cal. yr BP and was also detected in Lake Nahuel Rucá (Fig. 54), where a shift to a *C. meneghiniana* and *A. granulata* diatom assemblage occurred c. 800 cal. yr BP (Stutz et al. 2010). In both cases, the changes in diatom assemblage may be related to higher nutrient and lower light availability, characteristic of turbid organic-rich lakes (Bennion et al. 2010). Synchronicity in the past responses of both lakes Lonkoy and Nahuel Rucá (as compared in Fig. 54) suggests an external cause rather than isolated responses to local conditions at each lake site. There are also similar responses in pollen, non-pollen palynomorphs and plant macrofossils in lakes Lonkoy, Nahuel Rucá (Fig. 54) and Hinojales (5 km north of Lake Nahuel Rucá; see Stutz et al. 2012), which indicate changes in nutrient availability during the Holocene.

Two environmental factors might have caused the observed changes. First, the full retreat of the sea to its present level may have decreased the amount of brine entering the basin so allowing the development of freshwater environments more suitable for the growth of *A. granulata*. Second, increases in precipitation might have triggered the shift towards permanent freshwater conditions in the lake basins, with the consequent development of macrophytes and increases in phytoplankton biomass. Recent pollen-based precipitation reconstructions for the southeastern Pampas propose values c. 200 mm lower than present at c. 1200 cal. yr BP, followed by a sudden increase of 150 mm by c. 1000 cal. yr BP (Peña 2012). This precipitation change might have carried sediments and nutrients from the surrounding catchment into the lake. As a result, light limitation would have induced a decrease in submerged macrophytes (see Fig. 54), causing a shift from macrophyte-dominated clear water to a microalgae dominated turbid state (Stutz et al. 2012). Moreover, the dominance of *A. granulata* also indicates a strong influence of wind on the lake catchments, which would have ensured the prevalence of a well-mixed water column and prevented the sinking of *A. granulata* cells.

The upper 50 cm of the core (DAZ III to V) showed an increase in the dominance of brackish epiphytic and benthic taxa, accompanied by a decrease in the relative abundance of the planktonic diatoms, *C. meneghiniana* and *A. granulata*, towards the top of the core. The dominant diatoms, i.e., *N. peregrina*, *C. placentula*, *N. amphibia*, *P. subsalina*, *P. brevistriata*, *S. elliptica* and *N. brasiliensis* var. *platensis*, are usually associated to periphytic and benthic habitats. Some species (i.e., *P. brevistriata*, *S. elliptica*) indicate higher nutrient loadings and hypereutrophic conditions (Van Dam et al. 1994, Brenner et al. 1996). Replacement of the planktonic meso- to eutrophic *Aulacoseira* taxa by small hypereutrophic fragilarioid taxa has been reported elsewhere (e.g., Stoermer et al. 1992, Brenner et al. 1996, Korponai et al. 2010) and interpreted as indicating human agricultural impact. Intensive farming activities have developed in the Pampas during the last century, leading to increased nutrient loads and inorganic turbidity in shallow lakes highly exposed to intense land use of their drainage basins (Rennella & Quirós 2006). Higher loading of sediment and wind-induced resuspension would reduce light penetration preventing the development of planktonic diatoms and allowing the expansion of tycho plankton (fragilarioid) taxa. Pollen and non-pollen palynomorphs also recorded the development of modern lake conditions in this zone, with a high diversity of emergent macrophytes and free-floating plant species. The low abundance of planktonic algae and the development of free-floating plants suggested by pollen analyses support the hypothesis of human impact in Lake Lonkoy (Stutz et al. 2012). A similar change was recorded in Lake Nahuel Rucá, where the top-most 20 cm were also interpreted as representing modern

lake conditions (Stutz et al. 2010), with a dominance of epiphytic and brackish diatom taxa (Fig. 54)

Conclusion

The regional synchronicity of changes in diatom assemblage composition evidenced by comparison of Lonkoy and Nahuel Rucá lake records supports the hypothesis of a predominance of external triggers over intrinsic processes as causes of the main paleoenvironmental changes. The main environmental forces affecting these lakes seem to be related indirectly to the Holocene marine transgression and to recent human impacts. In addition to the evidence provided here, it remains imperative to increase the number of records in order to evaluate the regional extension and magnitude of these changes during the Holocene.

Besides the coincidence in the main shifts in the diatom composition between Lonkoy and Nahuel Rucá lake cores, the records also revealed variations of lower magnitude and specific differences between the lakes, the significance of which cannot yet be clearly addressed. The observed patterns are probably related to intrinsic differences in the nature and variability of the lakes of the region, which vary widely in their seasonal and interannual dynamics. Little is known about the modern dynamics of diatom communities inhabiting these lakes and, more importantly, about the patterns of distribution and preservation of their remains in surface sediments. In fact, the degree to which seasonal and long-term changes in diatom assemblages (as well as other biological indicators) are recorded in modern lakes is poorly known. Moreover, taphonomic alterations need to be addressed. Recent studies have demonstrated biases in the fossil diatom record associated with silica dissolution, which can be particularly important in saline lakes (Flower & Ryves 2009, Ryves et al. 2009). Hence, although the complex nature of pampean shallow lakes poses great challenges for paleolimnologists, it also opens the way to explore new and promising lines of work including better integration of ecological and paleoecological studies.

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