

## **Diatoms at >5000 Meters in the Quelccaya Summit Dome Glacier, Peru**

Authors: Fritz, Sherilyn C., Brinson, Bruce E., Billups, W. E., and Thompson, Lonnie G.

Source: Arctic, Antarctic, and Alpine Research, 47(2) : 369-374

Published By: Institute of Arctic and Alpine Research (INSTAAR), University of Colorado

URL: <https://doi.org/10.1657/AAAR0014-075>

---

BioOne Complete ([complete.BioOne.org](https://complete.BioOne.org)) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at [www.bioone.org/terms-of-use](http://www.bioone.org/terms-of-use).

Usage of BioOne Complete content is strictly limited to personal, educational, and non-commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

---

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

# Diatoms at >5000 meters in the Quelccaya Summit Dome Glacier, Peru

Sherilyn C. Fritz<sup>1,4</sup>

Bruce E. Brinson<sup>2</sup>

W. E. Billups<sup>2</sup> and

Lonnie G. Thompson<sup>3</sup>

<sup>1</sup>Department of Earth and Atmospheric Sciences and School of Biological Sciences, 214 Bessey Hall, University of Nebraska–Lincoln, Lincoln, Nebraska 68588-0340, U.S.A.

<sup>2</sup>Department of Chemistry and Richard E. Smalley Institute for Nanoscale Science and Technology, Rice University, 6100 South Main Street, Houston, Texas 77005, U.S.A.

<sup>3</sup>Byrd Polar and Climate Research Center and School of Earth Sciences, 275 Mendenhall Laboratory, 125 South Oval Mall, Ohio State University, Columbus, Ohio 43210, U.S.A.

<sup>4</sup>Corresponding author: sfritz2@unl.edu

## Abstract

Diatoms were found in late Holocene age ice-core samples recovered from the Quelccaya Summit Dome in the tropical Andes of Peru and were imaged by environmental scanning electron microscopy and identified. Freshwater diatoms in the genera *Hantzschia*, *Pinnularia*, and *Aulacoseira* were the most common taxa in the samples and indicate a freshwater source for the material, which also is suggested by the presence of the freshwater alga *Volvox*. The overall species composition of the diatoms suggests that the majority of taxa originated from a high-elevation lake or wetland in the cordillera surrounding the ice cap. The abundant diatom valves, up to 70  $\mu\text{m}$  in size, likely were transported to the ice via wind.

DOI: <http://dx.doi.org/10.1657/AAAR0014-075>

## Introduction

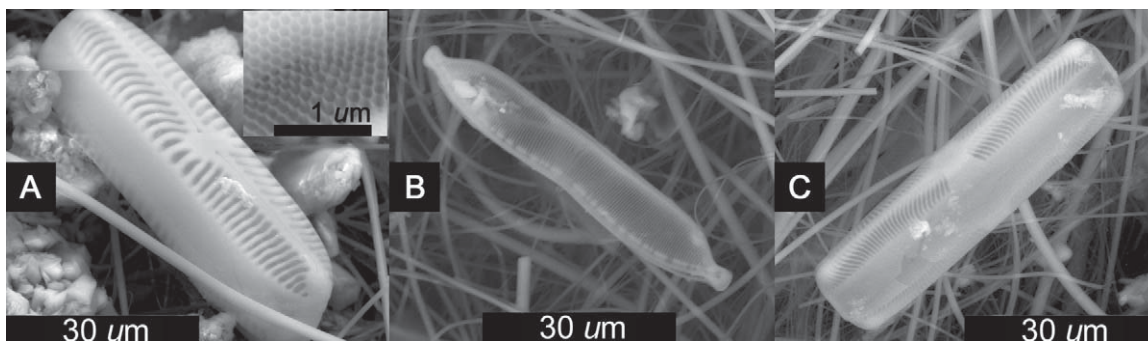
The analysis of ice cores from glaciers and ice caps in polar and alpine regions of the world has generated evidence of climate and environmental change associated with both natural and anthropogenic activities (Thompson et al., 2006). In addition to soluble isotopic and chemical evidence of changes in climate and atmospheric chemistry, ice cores also contain particulate material of both inorganic and biogenic origins that can provide insight into changes in land-surface cover and dynamics, including changes in dust production, biomass burning, and volcanic activity. Particulates trapped in ice also may reflect changes in atmospheric circulation patterns that affect long-distance transport of compounds from the continents or marine realm and their incorporation into glacial ice. In polar and high-latitude ice cores, the biological remains of microbes, including diatoms and other algae, have been reported in significant concentrations in glacier ice. In Greenland ice cores, for example, peaks in freshwater diatom concentrations are correlated with peaks in dust, suggesting that the diatoms were transported to the ice with dust from distant continental sources (Gayle et al., 1998; Donarummo et al., 2003). In various Antarctic ice cores, both freshwater and marine taxa have been identified and similarly attributed to eolian deposition (Burckle et al., 1988; Kellogg and Kellogg, 1996; Barrett, 2013).

The occurrence of diatoms and other microbes in glacier ice not only provides information about changes in source materials and their transport but also potentially provides useful information about the extent to which microorganisms are dispersed, which is central to understanding microbial biogeography (Fontaneto, 2011). Commonly it is assumed that microbes are widely dispersed (Fenchel and Finlay, 2004), yet many taxa have restricted rather than cosmopolitan distributions, suggestive of some sort of disper-

sal limitation (Telford et al., 2006; Boo et al., 2010). Contemporary studies of Antarctic snow show eolian dispersal of diatoms from marine sources over distances of 50 km (Budgeon et al., 2012) and have documented transport of centric diatoms up to 40  $\mu\text{m}$  in diameter and pennate taxa >100  $\mu\text{m}$  (McKay et al., 2008), although there is no evidence that these cells were viable during transit or at deposition.

The Quelccaya Ice Cap (13°56'S; 70°50'W, 5670 m a.s.l.) is located in the tropical Andes of southern Peru. During scanning electron microscope (SEM) analysis (Goldstein et al., 1992) of an ice core from the Quelccaya Summit Dome (QSD) for novel carbon nanomaterials derived from the burning of fossil fuels or through natural sources, we were surprised to find that the glacier ice was replete with freshwater diatoms. Although wind-blown diatoms carried in dust have been found in polar and high-latitude glaciers and ice caps (Harper and McKay, 2010), there are no prior reports of diatoms in glacial ice from tropical regions. In this article, we present SEM images and identifications of diatoms recovered from three core depths in the Quelccaya Summit Dome and make preliminary observations about their source and transport.

Diatom studies in tropical South America, particularly the tropical Andes, have a long and rich tradition extending back to the early 20th century, including explorations by Frenguelli (Frenguelli, 1939), the Percy Sladen Expedition (Tutin, 1940), and the Catherwood Expedition (Patrick, 1966). More recent studies include a flora of the entire Andean cordillera (Rumich and Lange-Bertalot, 2000) and various local investigations of specific diatom groups or habitats (Theriot et al., 1985; Tapia et al., 2004; Díaz and Maidina, 2005; Morales and Vis, 2007; Morales et al., 2012; Blanco et al., 2013; Montoya-Morena et al., 2013; Morales et al., 2014). Yet given the diverse range of habitats and the ex-



**FIGURE 1.** Environmental scanning electron microscope (ESEM) images of pennate diatoms observed in QSD1, QSD2, and QSD3. (A) *Pinnularia borealis*,  $59 \times \sim 12 \mu\text{m}$ . The inset shows nanoscale areolae within the striae, B) *Hantzschia amphioxys*,  $58 \times 9 \mu\text{m}$ , C) *Pinnularia* sp.,  $47 \mu\text{m}$ .

tensive area, the flora of the tropical Andes remains poorly documented, and only a few modern studies include documentation of the diatoms using modern advances in imaging technology.

## Methods

The samples reported on here are from an ice core collected in 2003 from the QSD, which was preserved at  $-30^\circ\text{C}$  until analysis (Thompson et al., 2013). The samples imaged by SEM were light brown filtrate spots  $\sim 1.5$  cm in diameter on  $\text{SiO}_2$  filter paper. Sections of analyte-bearing filter paper were mounted without further modification. Cylindrical fibers observed in the SEM images are the  $\text{SiO}_2$  filter material.

Samples evaluated in this work are identified as QSD1, QSD2, and QSD3 from core depths (and ages) of 146.23–146.80 m (A.D.  $1161\text{--}1176 \pm 3$  yr), 156.22–156.94 m (A.D.  $807\text{--}837 \pm 5$  yr), and 163.88–164.98 m (A.D.  $460\text{--}511 \pm 10$  yr), respectively. The ages of the upper samples were based on layer counting in sections of the core to  $\sim 160$  m (A.D. 683) (Thompson et al., 2000). The high annual accumulation rate ( $\sim 1200$  mm w.e. per year) and distinct seasonality of precipitation result in seasonal variations in mineral dust and stable isotopes of oxygen ( $\delta^{18}\text{O}$ ), as well as visible annual dust layers, which enable establishment of accurate annual layer counting over much of the core. These dry season dust bands also are visible on a crevasse wall of the Quelccaya ice cap (Thompson et al., 2013). The seasonality of the insoluble dust concentrations remains easily detectable with depth, even as the thinning becomes exponential. However, seasonal variations in  $\delta^{18}\text{O}$  become muted by diffusion with increasing depth. Thus, in the lower portions of the core, the ages were determined using a polynomial fit to the age/depth relationship, which gave a bottom date for the core of A.D. 226.

An FEI Quanta 400 environmental scanning electron microscope (ESEM) (Hillsboro, Oregon) was operated at 20 kV in wet mode (2–3 torr  $\text{H}_2\text{O}$ ). The ESEM was equipped with a EDAX™ (Trenton, New Jersey) energy dispersive spectrometer (EDS) fitted with a Super UTW™ 0.3 nm window, and a SiLi detector was operated in “spot” mode, utilizing 60 live second acquisition periods with dead times of  $\sim 25\%$ . Quantitative elemental analysis utilized the ZAF method (Goldstein et al., 1992). Elemental compositions are reported in atomic percent.

Diatom identifications of the SEM images were made with reference to regional floras (Rumich and Lange-Bertalot, 2000; Metzeltin, 2007; Blanco et al., 2013), as well as European (Krammer and Lange-Bertalot, 1986–1991, 1992) and North American (Patrick and Reimer, 1966; Camburn and Charles, 2000; Spaulding et al., 2010) floras.

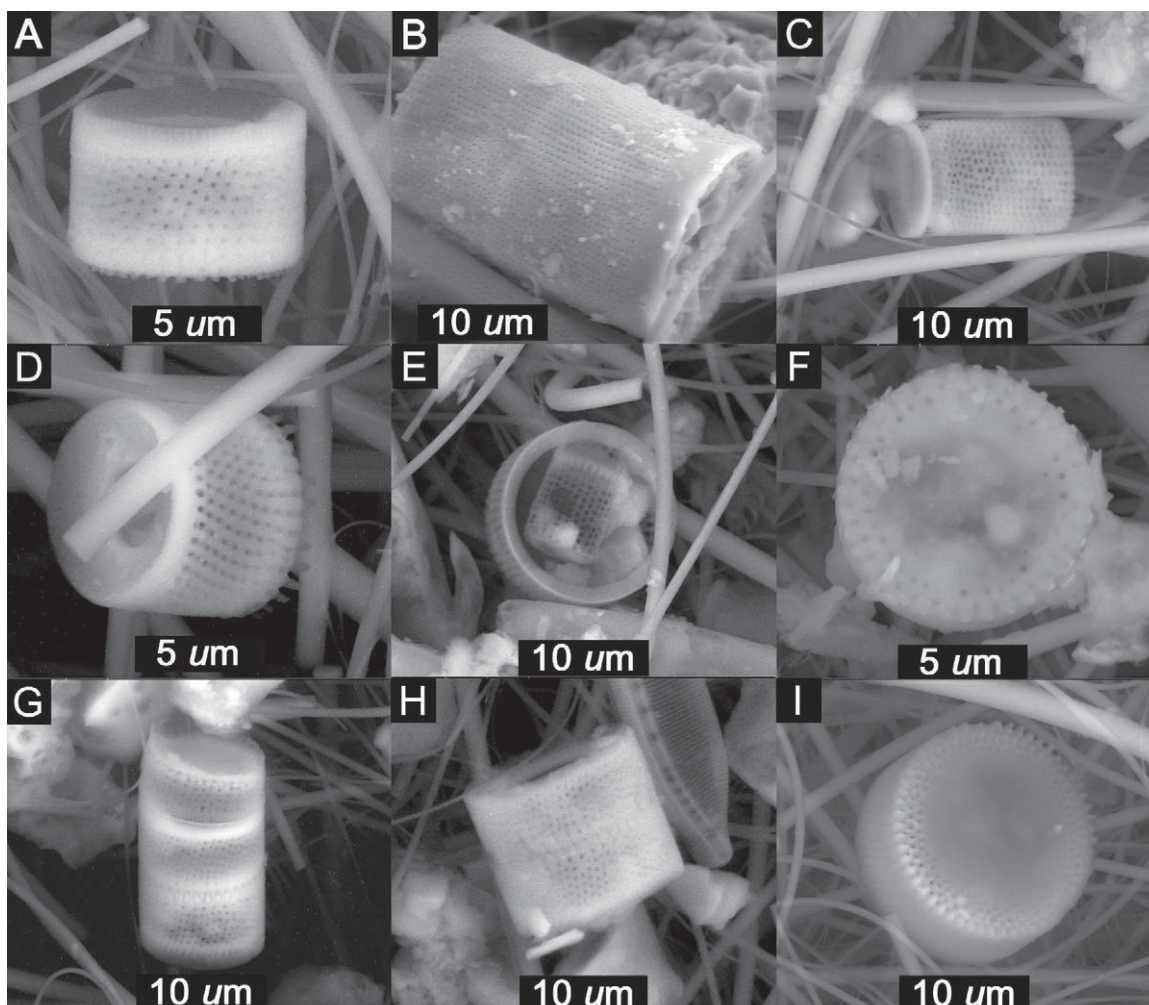
## Results and Discussion

The discovery of diatoms in the ice-core samples was a serendipitous by-product of SEM imaging of samples for carbon nanomaterials, and hence the observations are neither quantitative nor exhaustive. Some diatoms were obscured in the filter paper matrix, and some were broken and not imaged. As a result, all possible species in the samples may not be presented in this assessment, and the data presented should be considered a sampling of the material rather than a statistically valid cross section. Nonetheless, the samples furnish useful information on the size range of diatoms transported in high-elevation settings, such as the tropical Andes, and the species composition provides some clues to possible source regions of the material.

Particle size in the analyzed samples ranged from 10s of nm to 10s of  $\mu\text{m}$ . The particle density was estimated to be 1000s of particles per ice core liter, while diatom counts were in the range of 250–500 valves per ice core liter. The diatoms in the ice samples were small to moderate in size relative to the typical distribution of freshwater diatoms and ranged from 10–70  $\mu\text{m}$  in length and 3–16  $\mu\text{m}$  in width. The pennate diatoms in QSD2 had the broadest range in size, whereas valves in QSD3 were typically the smallest.

Three diatom genera (*Pinnularia*, *Hantzschia*, *Aulacoseira*) were common and frequently observed in the samples (Figs. 1 and 2). *Pinnularia borealis* was the most common taxon overall, and *Hantzschia amphioxys* and *Aulacoseira* also occurred in each sample. These common taxa also are found in ice cores from polar and high-latitude regions where diatoms have been observed and have been associated with long-distance eolian transport (Donarummo et al., 2003; Harper and McKay, 2010; Papina et al., 2013). Additional diatom fragments observed in QSD1, perhaps unique to QSD1, were indistinct and did not permit definitive identification. Figures 3 and 4 illustrate pennate diatoms apparently unique to samples QSD2 and QSD3, respectively.

The ecological affinities of the diatoms suggest that the valves originated from freshwater lakes, wetlands, or wet soils. The fresh-

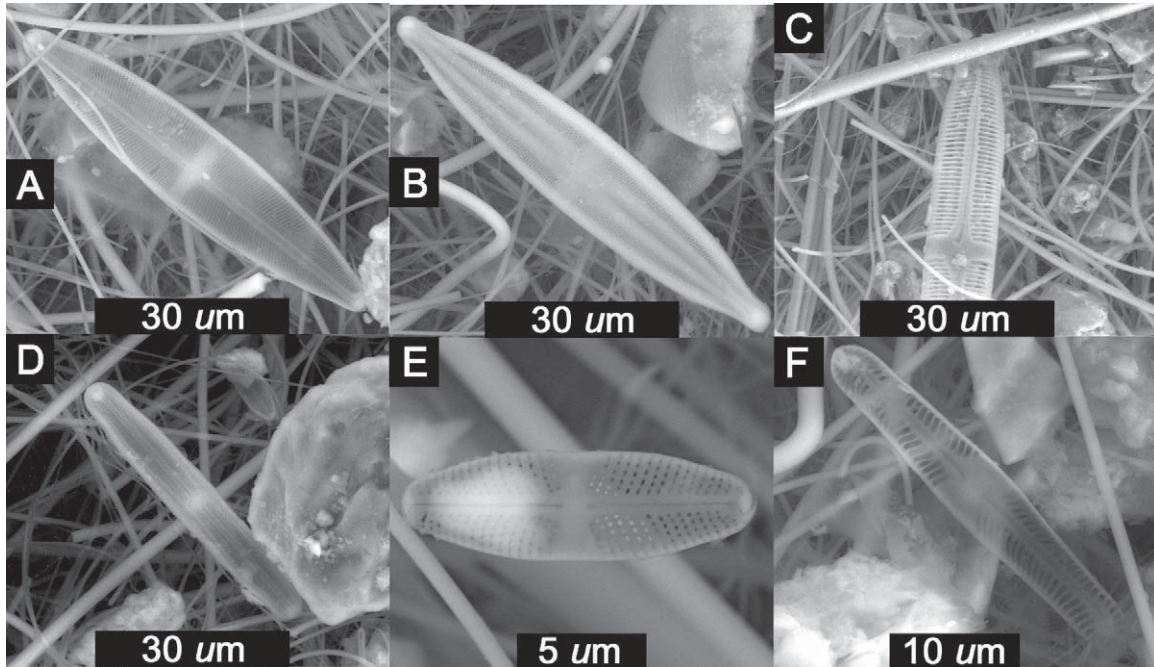


**FIGURE 2.** *Aulacoseira* valves (centric diatoms) observed in (A–C) QSD1, (D–F) QSD2, and (G–I) QSD3. Parts A, D, and F–I are *Aulacoseira alpigena*; others are *Aulacoseira* sp.

water inference is supported by the presence of *Volvox*, a green freshwater alga (Maberly et al., 1994) that was observed in QSD2 and QSD3 (Fig. 5, part A). The majority of other taxa in the samples suggest that the source freshwaters for the diatoms had low alkalinity and low nutrient concentrations. In particular, *Brachysira vitrea*, *Eunotia* sp., *Stauroneis* sp., and *Aulacoseira alpigena* are typical of fresh clearwater lakes that have low alkalinity (Camburn and Charles, 2000). *Aulacoseira* species often are planktic and occur during periods when the water column is not thermally stratified as a result of some combination of cool temperatures, strong winds, and/or shallow depth. In some cases, *Aulacoseira* species are tychoplanktic and grow in chains attached to shallow-water substrates, including plants, rocks, and mud. Among the other taxa, *Hantzschia amphioxys* is an aerophilous species that grows in wet soils or other subaerial habitats, and *Pinnularia borealis* is a common benthic taxon that is found in shallow flowing or standing waters, as well as in subaerial habitats, such as wet soils, mosses, or rock substrates. One likely scenario is that the diatoms found in the Quelccaya ice originated in nearby high-elevation lakes or wetlands, which are abundant on the slopes surrounding the ice cap. The proximate location is suggested by the abundance of diatoms in the analyzed samples and by the presence of taxa characteristic

of alpine lakes and wetlands, such as *Brachysira vitrea*, *Eunotia* sp., *Stauroneis* sp., and *Aulacoseira alpigena*. In addition, the preservation of the valves is generally excellent, which suggests the transport of recently deposited material from a lake or wetland, rather than long-distance transport of dust from older exposed sources, such as the southern Altiplano (Gaiero et al., 2013). Yet, two of the taxa (*Hantzschia amphioxys*, *Pinnularia borealis*) have been reported in global dust sources; thus, long-distance dispersal from a distant source for some of the valves cannot be ruled out.

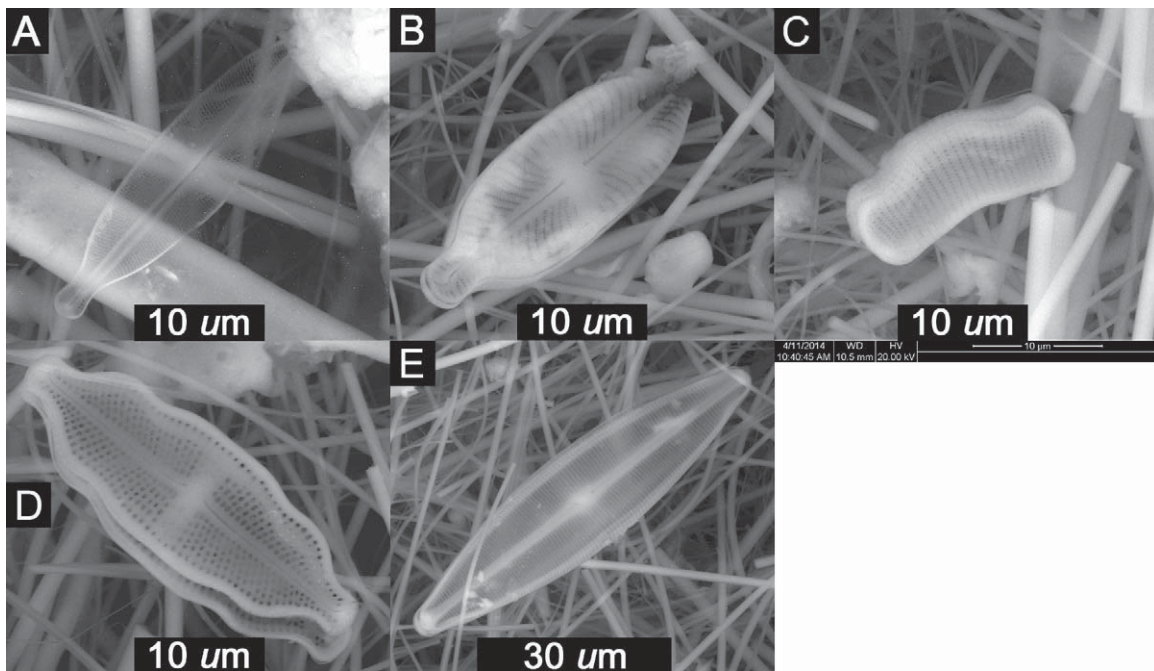
In addition to the diatoms, the filtrate samples included numerous discrete aluminosilicate particles and aggregates that contain C, Ca, Fe, K, Mg, P, Na, Ti, as well as non-diatomaceous silica structures that may have biological origins. Morphologically and elementally the filtrates were similar across all samples. Excluding a few Fe-bearing aggregates, only three non-diatomaceous particles with a recognizable crystal form were larger than 1  $\mu\text{m}$ . This suggests the predominance of particles with inorganic origins that have not experienced pressures and temperatures adequate for crystallization. Thus, the particles likely do not have origins deep within the earth, for example from volcanic eruptions, an observation that is consistent with the hypothesis of materials transported to the ice from surface deposits by wind.



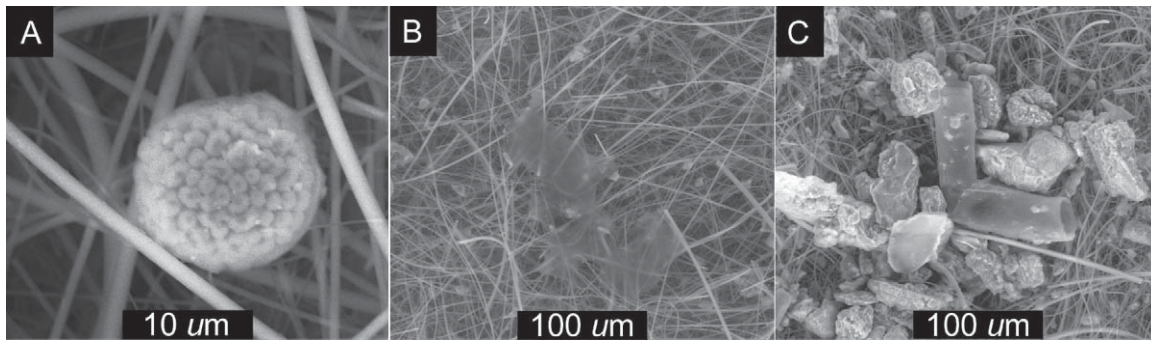
**FIGURE 3.** ESEM images of pennate diatoms found in QSD2. (A) *Stauroneis* sp. cf. *S. phoenicenteron*,  $66 \times 13.2 \mu\text{m}$ ; (B) *Stauroneis* sp.,  $72 \times 14 \mu\text{m}$ ; (C) *Caloneis* sp.,  $\sim 66 \times 10.8 \mu\text{m}$ ; (D) *Neidium bisulcatum*,  $46.2 \times 7 \mu\text{m}$ ; (E) *Achnanthes* sp. cf. *A. taylorensis*,  $12.8 \times 3.9 \mu\text{m}$ ; (F) *Pinnularia appendiculata*,  $33 \times 5 \mu\text{m}$ .

Electron beam transparent high-carbon content masses (ETCM, Fig. 5, part B) and other unidentified, but highly structured, silicate objects (not shown) also were observed in the samples. ETCM material was occasionally associated with diatoms, resulting in diffuse images, and the electron transparency of these

carbon masses results in significant  $\text{SiO}_2$  contributions from the silica filter paper to the EDS spectra. A quantitative carbon content of these objects could not be determined, but with the substrate contribution to the EDS spectra, these masses still returned >50% carbon. Particles in general, including diatoms, returned



**FIGURE 4.** ESEM images of pennate diatoms found in QSD3. (A) *Brachysira vitrea*,  $28 \times 6.5 \mu\text{m}$ ; (B) *Placoneis elginensis*,  $\sim 30 \times 10.3 \mu\text{m}$ ; (C) *Eunotia* sp. cf. *E. tenella*,  $19.7 \times 6.3 \mu\text{m}$ ; (D) *Luticola* sp. cf. *L. nivalis*,  $31 \times 10.5 \mu\text{m}$ ; (E) *Craticula* sp.,  $65 \times 15.5 \mu\text{m}$ .



**FIGURE 5.** ESEM Images of (A) *Volvox* (green algae); (B) irregular e-beam transparent carbon masses; and (C) 60% carbon tubes.

up to 10% carbon, whereas EDS spectra from a Si test wafer did not return a carbon signal. Two large tubes measuring  $\sim 85 \mu\text{m} \times 30 \mu\text{m}$  in diameter were shown to contain 60% carbon (Fig. 5, part C) and likely have a biological origin. No other well-defined, high carbon content particles were observed.

## Conclusions

Diatoms occur in glacial ice cores at an elevation of 5670 m a.s.l. in the Quelccaya Summit Dome ice field in the tropical Andes of Peru. The species composition of diatoms recovered from the ice indicates that most of the species originated from a dilute freshwater lake or wetland, and the excellent valve preservation suggests a local source rather than long-distance transport of dust from areas, such as the Southern Altiplano. Some taxa are common to all samples, while others are unique to individual samples. This variation probably reflects temporal changes in regional lacustrine diatom communities over the  $\sim 700$  year span of the samples. The observations provide useful floristic information on diatom distribution in a relatively poorly documented region and also provide constraints on the size range of organisms that are transported by wind in similar high-elevation settings. The observations also suggest the potential for analysis of diatoms in future ice core studies, where shifts in species composition may provide evidence on local climate or environmental change that complements the other materials identified in the ice core record.

## Acknowledgments

We would like to thank the Welch Foundation (C-0490) for financial support, the Byrd Polar and Climate Research Center for providing samples, and the Shared Equipment Authority at Rice University for use of their instrumentation suite. National Science Foundation (EAR)-1251678 to Fritz supported manuscript preparation.

## References Cited

- Barrett, P. J., 2013: Resolving views on Antarctic Neogene glacial history—the Sirius debate. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh*, 104: 31–53.
- Blanco, S., Álvarez-Blanco, I., Gejudo-Figueiras, C., De Godos, I., Bécares, E., Munoz, R., Guzman, H. O., Vargas, V. A., and Soto, R., 2013: New diatom taxa from high-altitude Andean saline lakes. *Diatom Research*, 28: 13–17.
- Boo, S. M., Kim, H. S., Shin, W., Boo, G. H., Cho, S. M., Jo, B. Y., Kim, J.-H., Yang, E. C., Siver, P. A., Wolfe, A. P., Bhattacharya, D., Andersen, R. A., and Yoon, H. S., 2010: Complex phylogeographic patterns in the freshwater alga *Synura* provide new insights into ubiquity versus endemism in microbial eukaryotes. *Molecular Ecology*, 19: 4328–4338.
- Budgeon, A. L., Roberts, D., Gasparon, M., and Adams, N., 2012: Direct evidence of aeolian deposition of marine diatoms to an ice sheet. *Antarctic Sciences*, 2012: 1–9.
- Burckle, L. H., Gayley, R. I., Ram, M., and Petit, J.-R., 1988: Diatoms in Antarctic ice cores: some implications for the glacial history of Antarctica. *Geology*, 16: 326–329.
- Camburn, K. E., and Charles, D. F., 2000: *Diatoms of Low-Alkalinity Lakes in the Northeastern United States*. Philadelphia: Academy of Natural Sciences, 152 pp.
- Díaz, C. P., and Maidina, N. I., 2005: *Diatomeas de los Salares Atacama y Punta Negra*. Santiago: Centro de Ecología Aplicada, 146 pp.
- Donarummo, J., Ram, M., and Stoermer, E. F., 2003: Possible deposit of soil dust from the 1930s U.S. Dust Bowl identified in Greenland ice. *Geophysical Research Letters*, 30: 1269.
- Fenchel, T., and Finlay, B., 2004: The ubiquity of small species: patterns of local and global biodiversity. *Bioscience*, 54: 777–784.
- Fontaneto, D., 2011: *The Biogeography of Microscopic Organisms: Is Everything Small Everywhere?* Cambridge: Cambridge University Press, 384 pp.
- Frenquelli, J., 1939: Diatomeas del Lago Titicaca. *Notas Museo La Plata*, 4: 175–196.
- Gaiero, D. M., Simonella, L., Gasso, S., Gili, S., Stein, A. F., Sosa, P., Becchio, R., Arce, J., and Marelli, H., 2013: Ground/satellite observations and atmospheric modeling of dust storms originating in the high Puna-Altiplano deserts (South America): implications for the interpretation of paleo-climatic archives. *Journal of Geophysical Research: Atmospheres*, 118: 3817–3831.
- Gayle, R. I., Ram, M., and Stoermer, E. F., 1998: Seasonal variations in diatom abundance and provenance in Greenland ice. *Journal of Glaciology*, 35: 290–292.
- Goldstein, J. I., Newbury, D. E., Echlin, P., Joy, D. C., Romig, A. D., Lyman, C. E., Fiori, C., and Lifshin, E., 1992: *Scanning Electron Microscopy and X-Ray Microanalysis*. New York: Plenum Press.
- Harper, M. A., and McKay, R. M., 2010: Diatoms as markers of atmospheric transport. In Smol, J. P., and Stoermer, E. F. (eds.), *The Diatoms: Applications for the Environmental and Earth Sciences*. Cambridge: Cambridge University Press, 552–559.
- Kellogg, D. E., and Kellogg, T. B., 1996: Diatoms in South Pole ice: implications for eolian contamination of Sirius Group deposits. *Geology*, 24: 115–118.
- Krammer, K., and Lange-Bertalot, H., 1986–1991: *Susswasserflora von Mitteleuropa. Bacillariophyceae*. Stuttgart: Gustav Fischer Verlag.

- Krammer, K., and Lange-Bertalot, H., 1992: *Pinnularia*. Stuttgart: J. Cramer, 353 pp.
- Maberly, S. C., Hurley, M. A., Butterwick, C., Corry, J. E., Heaney, S. I., Irish, A. E., Jaworski, G. H. M., Lund, J. W. G., Reynolds, C. S., and Roscoe, J. V., 1994: The rise and fall of *Asterionella formosa* in the South Basin of Windermere: analysis of a 45-year series of data. *Freshwater Biology*, 31: 19–34.
- McKay, R. M., Barrett, P. J., Harper, M. A., and Hannah, M. J., 2008: Atmospheric transport and concentration of diatoms in surficial and glacial sediments in the Allan Hills, Transantarctic Mountains. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 260: 168–183.
- Metzeltin, D., 2007: Tropical Diatoms of South America, II: Special Remarks on Biogeographic Disjunctions. Ruggell, Liechtenstein: A.R.G. Gantner Verlag Kommanditgesellschaft.
- Montoya-Morena, Y., Sala, S., Vouilloud, A., Aguirre, N., and Plata, Y., 2013: Lista de las diatomeas de ambientes continentales de Colombia. *Biota Colombiana*, 14: 13–78.
- Morales, E. A., and Vis, M. L., 2007: Epilithic diatoms (Bacillariophyceae) from cloud forest and alpine streams in Bolivia, South America. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 156: 123–155.
- Morales, E. A., Novais, M. H., Chavez, G., Hoffmann, L., and Ector, L., 2012: Diatoms (Bacillariophyceae) from the Bolivian Altiplano: three new araphid species from the Desaguadero River draining Lake Titicaca. *Fottea*, 12: 41–58.
- Morales, E. A., Rivera, S. F., Wetzel, C. E., Novais, M. H., Hamilton, P. B., Hoffmann, L., and Ector, L., 2014: New epiphytic araphid diatoms in the genus *Ulnaria* (Bacillariophyta) from Lake Titicaca, Bolivia. *Diatom Research*, 29: 41–45.
- Papina, T., Blyakharchuk, T. A., Eichler, A., Malygina, N., Mitrofanova, E., and Schwikowski, M., 2013: Biological proxies recorded in a Belukha ice core, Russian Altai. *Climate of the Past*, 9: 2399–2411.
- Patrick, R., 1966: *The Catherwood Foundation Peruvian-Amazon Expedition*. Philadelphia: Academy of Natural Sciences.
- Patrick, R., and Reimer, C. W., 1966: *The Diatoms of the United States*. Philadelphia: Academy of Natural Sciences, 688 pp.
- Rumich, U., and Lange-Bertalot, H., 2000: *Diatomeen der Anden*. Ruggell, Liechtenstein: A.R. Gantner Verlag K.G., 673 pp.
- Spaulding, S. A., Lubinski, D. J., and Potapova, M., 2010: Diatoms of the United States, <http://westerndiatoms.colorado.edu>.
- Tapia, P. M., Theriot, E. C., and Fritz, S. C., 2004: Distribution and morphometric analysis of *Cyclostephanos andinae* comb. nov, a planktonic diatom from the central Andes. *Diatom Research*, 19: 311–327.
- Telford, R. J., Vandvik, V., and Birks, H. J. B., 2006: Dispersal limitations matter for microbial morphospecies. *Science*, 312: 1015.
- Theriot, E., Carney, H. J., and Richerson, P. J., 1985: Morphology, ecology and systematics of *Cyclotella andina* sp. nov. (Bacillariophyceae) from Lake Titicaca, Peru-Bolivia. *Phycologia*, 24(4): 381–387.
- Thompson, L. G., Mosley-Thompson, E., and Henderson, K. A., 2000: Ice core paleoclimate records in tropical South America since the Last Glacial Maximum. *Journal of Quaternary Science*, 15: 377–394.
- Thompson, L. G., Mosley-Thompson, E., Brecher, H., Davis, M., Leon, B., Les, D., Lin, P.-N., Mashiotta, T., and Mountain, K., 2006: Abrupt tropical climate change: past and present. *Proceedings of the National Academy of Science*, 103: 10536–10543.
- Thompson, L. G., Mosley-Thompson, E., Davis, M. E., Zagorodnov, V. S., Howat, I. M., Mikhailenko, V. N., and Lin, P.-N., 2013: Annually resolved ice core records of tropical climate variability over the past ~1800 years. *Science*, 340: 945–950.
- Tutin, T. G., 1940: The algae: reports of the Percy Sladen Trust Expedition to Lake Titicaca in 1937. *Linnean Society of London, Transactions, Series 3*, 1(11): 191–202.

MS accepted January 2014