Freshwater diatoms in the Sajama, Quelccaya, and Coropuna glaciers of the South American Andes

D. Marie Weide , Sherilyn C. Fritz, Bruce E. Brinson, Lonnie G. Thompson & W. Edward Billups

Published online: 17 Jul 2017.

Submit your article to this journal ⧉

Article views: 6

View related articles ⧉

View Crossmark data ⧉

Taylor & Francis
Taylor & Francis Group

Check for updates

Freshwater diatoms in the Sajama, Quelccaya, and Coropuna glaciers of the South American Andes

D. MARIE WEIDE [1]*, **SHERILYN C. FRITZ**[1], **BRUCE E. BRINSON**[2], **LONNIE G. THOMPSON**[3] & **W. EDWARD BILLUPS**[2]

[1]*Department of Earth and Atmospheric Sciences, University of Nebraska-Lincoln, Lincoln, NE, USA*
[2]*Department of Chemistry, Rice University, Houston, TX, USA*
[3]*School of Earth Sciences and Byrd Polar and Climate Research Center, The Ohio State University, Columbus, OH, USA*

Diatoms in ice cores have been used to infer regional and global climatic events. These archives offer high-resolution records of past climate events, often providing annual resolution of environmental variability during the Late Holocene. Recently, the first low-latitude tropical diatoms were described from the Quelccaya Summit Dome. Here, we document diatoms observed in ice cores from Quelccaya, spanning AD 1300 to 1815, along with those from two additional glaciers (Coropuna, and Sajama glaciers) in the tropical Andes, spanning AD 1764 to 1814. Diatom assemblages recovered from these three sites were rare, but differ in abundance and species composition through time. Assemblages are characterized by cosmopolitan and aerophilic species, mostly pennate diatoms. There were 44 taxa in all, with *Pinnularia* cf. *borealis* Ehrenberg being the most common species encountered in the samples. Eleven taxa were found at all three sites. Both Coropuna and Sajama had taxa that were unique to these locations, whereas Quelccaya had no unique taxa. Due to the rarity of diatoms and the cosmopolitan nature of the dominant species, it is not possible to determine their origin, limiting their utility in paleoclimate reconstructions.

Keywords: *ice cores, tropical Andes, aerophilic diatoms, bacillariophyceae*, Pinnularia borealis *Ehrenberg, dust transport*

Introduction

Ice cores from the Eastern and Western Cordilleras of the tropical Andes offer insights into past climate and environments (Thompson et al. 1985, 1986, 2013, Liu et al. 2007, Herreros et al. 2009, Reese et al. 2013). Particulate matter preserved in dust layers in these ice cores includes diatoms (Thompson et al. 1994, Fritz et al. 2015), which may provide clues to climatic patterns in the southern hemisphere, environmental dynamics associated with the accumulation of the ice, as well as information on microorganismal dispersal mechanisms across extreme barriers like the Andes.

Wind has long been known to distribute dust and associated microscopic particles, which include pollen and microorganisms, long distances (Harper 1999, Finlay 2002). Aeolian deposition of diatoms in ice cores from polar areas, including Greenland and Antarctica, is well documented (Burckle et al. 1988, Gayley et al. 1989, Donarummo et al. 2003). In addition, aeolian-deposited diatoms have been used as environmental proxies. Pokras & Mix (1985) used freshwater diatoms from deep-sea sediments to track long-term climate variability in tropical Africa since the Last Glacial Maximum.

Recent research has shown that, at least in some cases, there are limits to the dispersal of microorganisms and that the distribution of microbes is influenced by both historical events and environmental conditions (Martiny et al. 2006). The factors that affect the dispersal of diatoms under different scenarios are still uncertain, but aeolian-distributed diatoms can increase our understanding of dispersal mechanisms. For example, Van Eaton et al. (2013) demonstrated that diatoms in tephra deposits originated from ancient Lake Huka, New Zealand, and had become incorporated into the ash plume as the volcano erupted through the lake bed. These diatoms were dispersed hundreds of kilometres from the source, but it is still unclear whether they would have been viable once deposited in their new environment.

There are still questions on the utility of the diatoms found in ice cores as proxies for paleoenvironmental reconstruction and biogeographical studies. Diatoms are a rare component of dust collected in atmospheric traps (Harper & McKay 2010), and, thus, may not be useful as proxies of past environment and climate. In addition, diatoms found in previous ice core studies (Donarummo et al. 2003, Harper & McKay 2010, Fritz et al. 2015) are

---

*Corresponding author. E-mail: dmarieweide@gmail.com

Fig. 1. Map of the study area.

mostly cosmopolitan aerophilic species, which may limit their utility as indicators of dispersal.

We used diatoms found in ice cores from three sites, two on the western boundary and one on the eastern boundary of the Altiplano, to explore the utility of diatoms within tropical ice cores as indicators of past climate and environment, as well as whether they can provide information on the likely source region of the diatoms. This study builds on a preliminary report on diatoms observed in the Quelccaya ice core (Fritz et al. 2015) and discusses diatoms found in two additional ice cores, Nevado Sajama and Nevado Coropuna.

Site descriptions

The glaciers included in this study are located in the tropical Andes of Peru and Bolivia (Fig. 1). The Andean cordillera is a volcanic arc that is located on the western edge of South America, extending from the western border of Venezuela down the Pacific coast to Patagonia at the southern tip of Argentina. Due to their height, the mountains obstruct atmospheric circulation of air masses between the Pacific and Amazon lowlands (Garreaud et al. 2003). The large internally drained basin known as the Altiplano is located between the Eastern and Western

Cordilleras in the Central Andes (66–71°W, 14–22°S, $\sim$3650–3900 m a.s.l.), covering parts of Peru, Bolivia, Argentina, and Chile (Argollo & Mourguiart 2000), with a gradient of decreasing precipitation from north to south (Condom et al. 2004). The Central Andes are characterized by steep elevational gradients, with the western slopes on the Pacific Coast having a steeper gradient than the eastern slopes. Cold-water upwelling in the Pacific results in cool sea-surface temperatures and aridity on the western slopes (Zhou & Lau 1998). The Eastern Central Andes are located adjacent to the relatively wetter Amazon lowlands. The dominant source of precipitation for the Central Andes is the Atlantic Ocean via the Amazon Basin (Baker et al. 2001).

Nevado Coropuna (15°33′S 72°39′W, 6450 m a.s.l.), located $\sim$155 km NW of Arequipa, Chile, is an inactive volcano in the Cordillera Ampato (Zagorodnov et al. 2005), on the western boundary of the Altiplano (Kuentz et al. 2007). Its area was 60.8 km² in 2000 (Racoviteanu et al. 2007). Precipitation is mainly from the east, with air masses originating in the tropical Atlantic Ocean, although infrequent air masses from the Pacific and southern South America can also affect this site. The majority ($\sim$70–90%) of annual precipitation ($\sim$700 mm yr^{-1}) falls during the austral summer (December through March) (Herreros et al.

Table 1. Ice core samples analysed in this study.

Site and sample ID	Core depth (m)	Age (AD)	Volume of water (mL)	Total valves observed	Valves/100 mL
Coropuna					
CCC111.74	111.74–111.85	1811	145	6	4.1
CCC113.12	113.12–113.23	1801	150	262	174.7
CCC117.68	117.68–117.81	1766	155	23	14.8
Quelccaya					
QSD97.49	97.49–97.64	1813	145	20	13.8
QSD98.98	98.98–99.09	1802	160	38	23.8
QSD103.59	103.59–103.77	1764–1765	155	30	19.4
QSD136.40	136.40–136.56	1410–1414	170	18	10.6
QSD138.65	138.65–138.88	1361–1366	160	11	6.9
QSD141.11	141.11–141.30	1306–1311	200	27	13.5
Sajama					
SJ51.99	51.99–52.14	1814	160	29	18.1
SJ53.30	53.30–53.43	1799	145	164	113.1
SJ55.90	55.90–56.15	1764	190	175	92.1

2009). The dry season is short, lasting June through August (Brack & Mendiola 2000). The average annual temperature is $< 6°C$ (Kuentz et al. 2007). The local vegetation is characterized by puna brava, a high-elevation environment with sparse vegetation. It is composed of mainly Apiaceae (*Azolla*) and Asteraceae, with common occurrences of marshes and peat bogs in glacially shaped valleys (Kuentz et al. 2007, 2011).

Nevado Sajama (18°06′S 68°53′W, 6542 m a.s.l.), an extinct volcano in the relatively dry Western Cordillera of Bolivia, approximately 150 km south of Lake Titicaca, is near the Chilean-Peruvian border (Vuille 1999, Liu et al. 2005) on the western boundary of the Altiplano. The approximate area of the glacier is $4 km^2$ (Williams & Ferrigno 1998). The mean annual temperature is $-12°C$, and the annual precipitation is $400 mm yr^{-1}$ (Hong et al. 2004). The dry season (May through October) is dominated by winds from the west, whereas the wet season (December through March) is dominated by winds from the east and northeast (Liu et al. 2005, Reese et al. 2013) (from the eastern Andean slopes and Amazon lowlands). It is during the wet season that accumulation occurs on the glacier (Reese et al. 2013). The environment is categorized as dry puna, which is dominated by Asteraceae and other small shrubs (Reese et al. 2013). *Bofedales*, or peat bogs, are common (Baied & Wheeler 1993, Reese et al. 2013).

Quelccaya is located in the Eastern Cordillera (13°56′ S, 70°50′ W, 5670 m a.s.l.) of Southern Peru and is the largest glacier in the tropics with an estimated area of $55 km^2$ (Thompson et al. 1985). The average annual temperature is $-3°C$ (Thompson et al. 1985). The annual precipitation is $700–1500 mm yr^{-1}$, with the majority ($\sim 80\%$) falling in the wet season (November–April) (Thompson et al. 1985, Reese & Liu 2002). The winds come from the east and northeast during the austral summer and from the west the remainder of the year. The vegetation is classified as super-puna and is marked by scant

small plants, especially *Plantago*, and shrubs, including *Polylepis* (Reese & Liu 2002).

Materials and methods

The diatom samples presented here were taken from ice cores recovered in 2003 from the Quelccaya Summit Dome (QSD) (Zagorodnov et al. 2005, Fritz et al. 2015), the Sajama Ice Cap (SJ) in 1997 (Hong et al. 2004, Liu et al. 2005), and the Coropuna Ice Cap (CCC) in 2003. Samples for diatom analysis were chosen based on dust layers thick enough to be seen without a microscope, maximizing the amount of dust in each sample. A total of 12 samples were analysed: 3 from CCC, 6 from QSD, and 3 from SJ (Table 1). The QSD samples were different to those discussed by Fritz et al. (2015). Ice core samples were melted and the water volume of each sample was measured in order to determine a simple concentration (number of valves per 100 mL) for each sample. Samples were then filtered through SiO_2 filter paper. The filter papers were transferred to scintillation vials, processed using 30% H_2O_2 to remove organic matter, and subsequently rinsed with deionized water to remove remaining chemical by-products. SEM images were obtained on a FEI Quanta 400 environmental microscope using wet mode (Hillsboro, Oregon) with EDAX™ (Trenton, New Jersey) energy-dispersive spectrometer with a Super UTW™ 0.3 nm window. Slides for each sample were made by placing aliquots of the suspended diatoms onto coverslips, and the dried samples were mounted in Naphrax (PhycoTech) (RI = 1.74). The entirety of each sample was mounted and counted. Diatoms were identified using a LEICA DMRX transmitted-light microscope fitted with a 100 × Phase contrast (N.A. = 1.40) oil immersion objective lens (magnification = 1000 ×). Diatom species identification used regional floras (Frenguelli 1939, 1941, Metzeltin & Lange-Bertalot 1998, Metzeltin et al. 2005, Metzeltin &

Lange-Bertalot 2007), as well as floras from both Europe and North America (Patrick & Reimer 1966, Krammer & Lange-Bertalot 1986–1991, Spaulding et al. 2010).

Ages of the QSD samples presented here, part of a core that spans the last 1800 cal years BP, were determined by counting distinct annual layers (for full discussion, see Thompson et al. 2013). The Sajama core was dated using ^{14}C from organic matter, ^{18}O isotopes, tritium calibrated layer counts of the top 100 years, and an ash horizon from the Huaynaputina volcanic event 1600 AD (see Thompson et al. 1998 for full discussion). The timescale development of the Coropuna ice core (CCC) is based on annual summer (wet) and winter (dry) seasonal oscillations in dust concentration and $\delta18O$ for the last 250 years. The twentieth century timescale is calibrated with the 1964/65 ^{3}H peak (residue from thermonuclear testing) at 38.5 m (Thompson et al. 2017).

Results

Diatoms were rare in these samples, and only one sample contained more than 200 valves. Only three samples (CCC113.12, SJ53.30, SJ55.90) contained more than 100 valves (Table 1). The remaining samples each contained less than 40 valves. Thus, with such low counts, percent abundance would not give a realistic representation of species abundance. Therefore, raw counts are presented, so as not to make species abundances appear larger than they are (Fig. 2).

The CCC and SJ core samples span the last half of the eighteenth century and first decade of the nineteenth century (AD 1764–1814), representing a period that spans approximately 50 years. The QSD core samples span the fourteenth through beginning of the nineteenth century (AD 1306–1813) (Table 1). The CCC111.74, QSD97.49, and SJ51.99 samples are dated to approximately AD 1813. CC2, QSD98.98, and SJ53.30 are dated to approximately AD 1800. Thus, the samples within these groups are approximately contemporaneous. CCC117.68, QSD103.59, and SJ55.90 are dated to approximately AD 1764. QSD136.40, QSD138.65, and QSD141.11 are dated to AD 1410, AD 1361, and AD 1306, respectively.

General trends

Overall, pennate diatoms dominate the assemblages, and centric species are very rare (Figs 3–20). Centric species make up only 3% of all observed diatoms, although centric valves were observed at all sites. The most common taxon in the samples (regardless of site) is *Pinnularia* cf. *borealis* Ehrenberg (27%). The other common diatoms include *Pinnularia* Ehrenberg spp. (19%), *Fragilaria* Lyngbye spp. (14%), *Hippodonta* Lange-Bertalot, Witkowski & Metzeltin spp. (7%), *Hantzschia* cf. *amphioxys* (Ehrenberg) Grunow (6%), and *Luticola* Mann spp. (5%). All sites contain the following species:
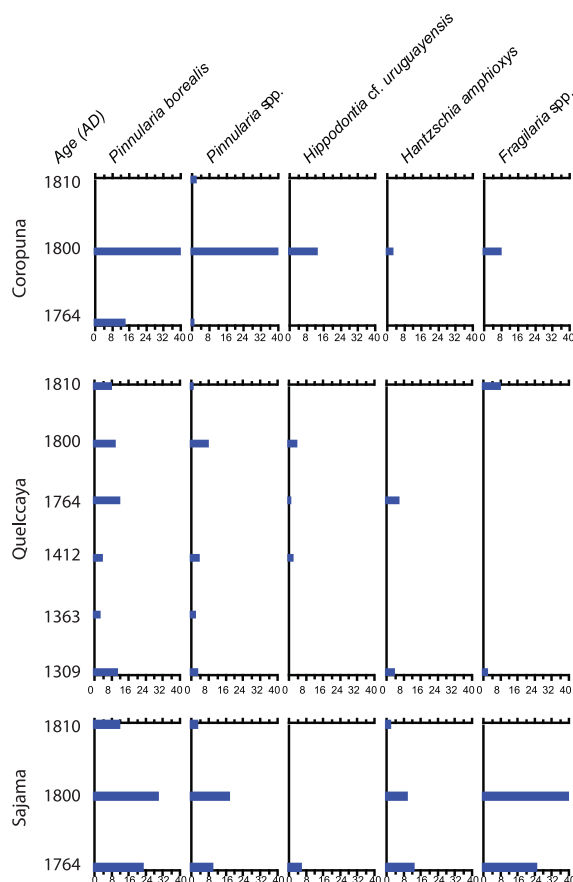

Fig. 2.   Raw counts of the dominant species in the ice core samples plotted through time. The *X*-axes are number of valves observed.

P. cf. *borealis*, *P.* cf. *borealis* var. *lanceolata* Hustedt, *Pinnularia microstauron* (Ehrenberg) Cleve, *Hippodonta* cf. *uruguayensis* Metzeltin, Lange-Bertalot & García-Rodríguez, *H.* cf. *amphioxys*, *Luticola* (sp. 3), and *Caloneis bacillum* (Grunow) Cleve. In addition, all sites contain at least one species from each of the following genera: *Aulacoseira* Thwaites, *Pinnularia*, *Epithemia* Kützing, and *Fragilaria*. Diatom species occurrences are summarized in Table 2. Chrysophyte cysts and phytoliths were also found at all sites (Figs 21–23).

Coropuna (CCC)

The Coropuna samples (CCC111.74, CCC113.12, and CCC117.68) contain a total of 31 taxa, including 12 that were unique to this site (Table 2). CCC shares more taxa in common with SJ (seven taxa) than with QSD (one taxon). Diatoms that are unique to this site are *Cavinula pseudoscutiformis* (Hustedt) Mann & Stickle (Fig. 20), *Cyclotella* (Kützing) Brébisson spp., *Cymbella* cf. *ventricosa* (C. Agardh) C. Agardh, *Diatoma* Bory de Saint-Vincent
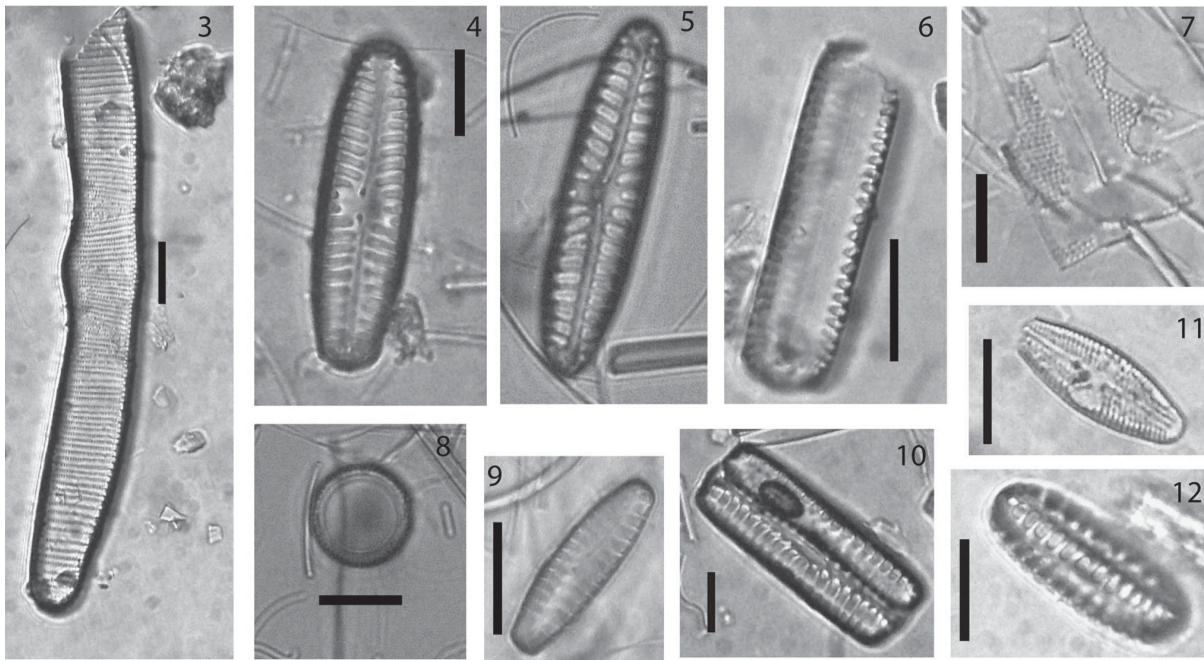
Figures 3–12. Light micrographs of diatoms observed in the ice cores. Fig. 3. *Eunotia* sp. Fig. 4. *P.* cf. *borealis* Fig. 5. *P.* cf. *borealis* Fig. 6. *P.* cf. *borealis* Fig. 7. *Stauroneis* sp. Fig. 8. *Aulacoseira* sp. Fig. 9. *P.* cf. *borealis* Fig. 10. *P.* cf. *borealis* Fig. 11. *Luticola* sp. Fig. 12. *P.* cf. *borealis*. Scale bars = 10 μm (Figs 3–7, Figs 9–12); 5 μm (Fig. 8).
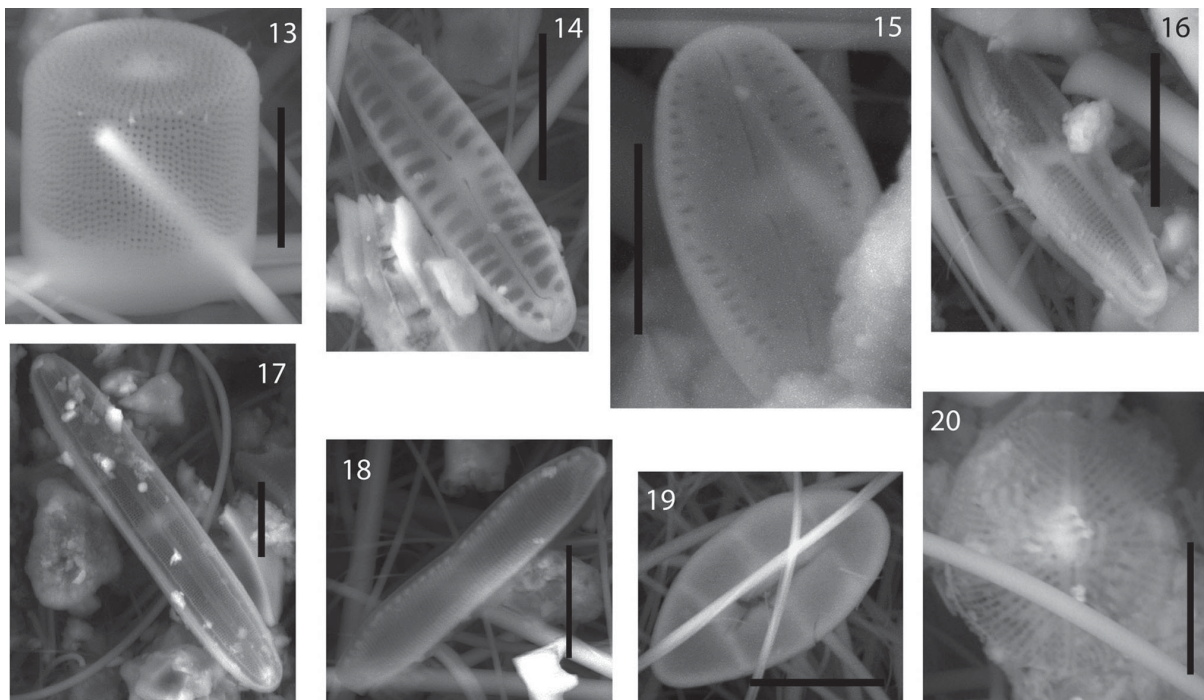
Figures 13–20. SEM images of diatoms observed in the ice cores. Fig. 13. *Orthoseira* cf. *roseana*. Fig. 14. *P.* cf. *borealis* Fig. 15. *Luticola* (sp. 3) Fig. 16. *Stauroneis phoenicenteron* Fig. 17. *Neidium sp*. Fig. 18. *Hantzschia* cf. *amphioxys* Fig. 19. *Diatoma* sp. Fig. 20. *Cavinula pseudoscutiformis*. Scale bars = 10 μm (Figs 13, 14, 16–19); 5 μm (Figs 15 and 20).

Table 2. Presence/absence data for species observed at Coropuna (CCC), Quelccaya (QSD), and Sajama (SJ).

Species	CCC	QSD	SJ	Subaerial/aerophilic
Aulacoseira spp.	X	X	X	
Caloneis bacillum	X	X	X	
Epithemia sp.	X	X	X	
Fragilaria spp.	X	X	X	
Hantzschia cf. *amphioxys*	X	X	X	X
Hippodonta cf. *uruguayensis*	X	X	X	
Luticola sp. 3	X	X	X	X
Pinnularia borealis var. *lanceolata*	X	X	X	X
Pinnularia microstauron	X	X	X	X
Pinnularia cf. *borealis*	X	X	X	X
Pinnularia spp.	X	X	X	
Aulacoseira alpigena	X	X		
Denticula		X	X	
Luticola spp.		X	X	
Pinnularia borealis var. *scalar*		X	X	X
Cocconeis placentula	X		X	
Eunotia spp.	X		X	
Fragilaria construens var. *exigua*	X		X	
Fragilaria pinnata	X		X	
Hippodonta spp.	X		X	
Navicula spp.	X		X	
Nitzschia spp.	X		X	
Cavinula pseudoscutiformis	X			X
Cyclotella spp.	X			
Cymbella cf. *ventricosa*	X			
Diatoma sp.	X			
Eunotia tenella	X			
Fragilaria pseudoconstruens	X			
Hantzschia cf. *linearis*	X			
Luticola nivalis	X			X
Neidium sp.	X			
Pinnularia cf. *bartii*	X			
Sellaphora spp.	X			
Stauroneis phoenicenteron	X			
Achnanthes sp.			X	
Eunotia species 1			X	
Fragilaria lapponica			X	
Fragilaria heidenii			X	
Hantzschia capitata			X	
Luticola cf. *mutica*			X	X
Luticola cf. *simplex*			X	X
Pinnularia lata			X	X
Pinnularia microstauron var. *angusta*	X		X	
Pseudostaurosira spp.			X	
Rhopalodia sp.			X	
Tryblionella sp.			X	

sp. (Fig. 19), *Eunotia tenella* (Grunow) Hustedt, *Fragilaria pseudoconstruens* Marciniak, *Hippodonta* cf. *linearis* (Østrup) Lange-Bertalot, Metzeltin & Witkowski, *Luticola nivalis* (Ehrenberg) Mann, *Neidium* Pfitzer sp. (Fig. 17), *Pinnularia* cf. *bartii* Metzeltin & Lange-Bertalot, *Sellaphora* Mereschkowsky sp., *Stauroneis phoenicenteron* (Nitzsch) Ehrenberg (Fig. 16).

Diatoms are rare (total 23 valves, 14.8 valves per 100 mL) in CCC117.68, of which the majority are *P*. cf. *borealis*, with a few *Pinnularia* and *Epithemia*. Diatom content increases drastically in CCC113.12 (total 262 valves, 174.7 valves per 100 mL), as do the number of taxa. *P*. cf. *borealis* comprises ∼23% of the assemblage, and unidentified *Pinnularia* spp. comprise 17%. *Hippodonta* species (*H*. *uruguayensis*, *H*. *capitata* (Ehrenberg) Lange-Bertalot, Metzeltin & Witkowski, and *H*. *linearis*) comprise 9%. This is also the only sample to contain *Cyclotella* spp. Diatom number decreased again in CCC111.74, with only two species, *Diatoma* sp. and *Pinnularia* sp., in the six valves observed (4.1 valves per 100 mL).

Quelccaya (QSD)

Diatoms were rare in the Quelccaya samples (QSD97.49, QSD98.98, QSD103.59, QSD136.40, QSD138.65, and QSD141.11), with a total of 15 taxa, none of which are unique to the site. The QSD samples share more common taxa with Sajama than Coropuna. *Pinnularia* spp., *P*. cf *borealis*, and *Fragilaria* spp. are the most common diatom taxa found at Quelccaya. The samples share 3 taxa with SJ and 12 taxa (*Aulacoseira alpigena* (Grunow) Krammer) with CCC.

QSD141.11 has five taxa and is dominated by *P*. cf. *borealis*, with lesser amounts of *Pinnularia* spp. and *H*. cf. *amphioxys*. Diatom counts and richness decrease in both QSD138.65 (four taxa, total 11 valves, 6.9 valves per 100 mL) and QSD136.40 (four taxa, total 18 valves, 10.6 valves per 100 mL). These samples are dominated by *P* cf. *borealis* and *Pinnularia* spp. In QSD103.59 (6 taxa, total 30 valves, 19.4 valves per 100 mL), diatom counts increase and *P*. cf. *borealis* and *H*. cf. *amphioxys* dominate. *Hippodonta uruguayensis*, *Epithemia* spp., and *Luticola* spp. also occur but are rare in this sample. Diatom counts reach their highest number (total 38 valves, 23.8 valves per 00 mL) in the Quelccaya samples in QSD98.98. This sample has four taxa and is dominated by *P*. cf. *borealis*, *Pinnularia* spp., and *H*. *uruguayensis*. In addition, it is the only Quelccaya sample to have *Luticola* (sp. 3). QSD97.49 has only four observed taxa, and the diatom valve count decreased again (total 20 valves, 13.8 valves per 100 mL). It is dominated by *Fragilaria* spp. and *P*. cf. *borealis*, with *Luticola* sp. and *Pinnularia* spp. being minor components.

Sajama (SJ)

The Sajama site (SJ51.99, SJ53.30, and SJ55.90) is characterized by 33 taxa, the largest number of all three sites. There are 12 unique taxa: *Achnanthes* Bory sp., *Eunotia* Ehrenberg (sp. 1), *F*. *lapponica* Grunow, *Fragilaria heidenii* Østrup, *Luticola* cf. *mutica* (Kützing) Mann, *Luticola* cf. *simplex* Metzeltin, Lange-Bertalot & García-Rodríguez, *Pinnularia lata* (Brébisson) Smith, *P*. *microstauron* var. *angusta*, *Pseudostaurosira* Williams & Round spp., *Rhopalodia* Muller sp., *Tryblionella* Smith sp. Sajama samples have seven taxa in common with Coropuna, and three taxa in common with QSD.
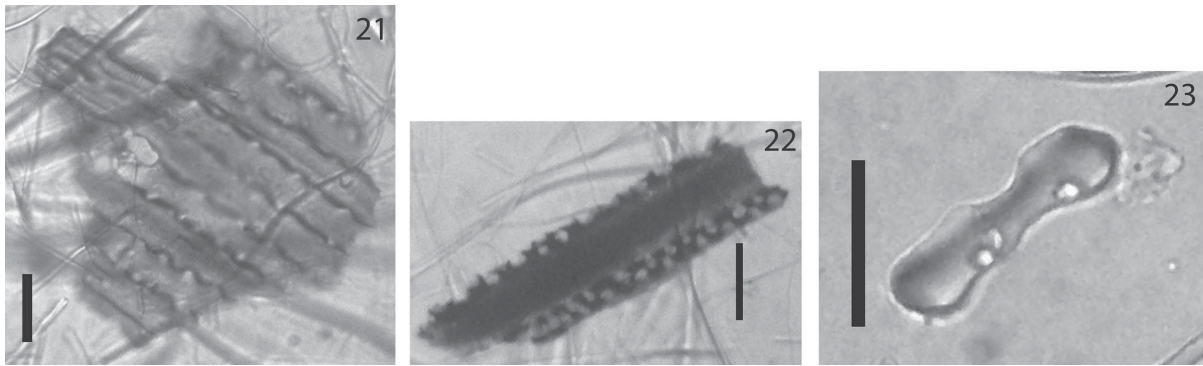
Figures 21–23.   Phytoliths observed in the ice cores. Scale bars = 5 μm.

SJ55.90 has the highest count, and second highest concentration (total 175 valves, 92.1 valves per 100 mL) from the Sajama core, and contained 20 taxa. It is dominated by *Pinnularia* spp. (27%), *Fragilaria* spp. (14%), and *P.* cf. *borealis* (13%). *Pinnularia microstauron*, *Hippodonta* spp., *H.* cf. *amphioxys*, and *Luticola* sp. total approximately 8% each. Diatom concentration is the highest in SJ53.30 (total 164 valves, 113.1 valves per mL), and the number of taxa observed increased slightly (24 taxa). This sample has higher numbers of *Pinnularia* spp., *P.* cf. *borealis*, and *Fragilaria* spp. The dominant taxon is *Fragilaria* spp., which includes *F. pinnata*, *Fragilaria construens* var. *exigua* (Smith) Schulz, *F. lapponica*, as well as unidentifiable *Fragilaria* fragments. Other taxa are *H.* cf. *amphioxys* (6%), *Hippodonta* spp. (4%), and *Luticola* spp. (3%). SJ51.99 shows a decrease in the total number of valves observed (29, 18.1 valves per 100 mL), the majority of which are *Pinnularia* spp., *P.* cf. *borealis*, and *H.* cf. *amphioxys*.

Discussion

The ice core diatoms presented here are low in abundance, which limits their use as a tool for environmental reconstructions. The diatom assemblages are composed of common benthic species found in freshwater environments. Eleven taxa are also subaerial/aerophilic taxa that can thrive in soil and drier conditions. These species include *P. microstauron*, *P. microstauron* var. *angusta*, *P. lata*, *L. simplex*, *L.* cf. *mutica*, *L. nivalis*, *Luticola* (sp. 3), *C. pseudoscutiformis*, *P.* cf. *borealis*, *P.* cf. *borealis* var. *scalaris* (Ehrenberg) Rabenhorst, *P.* cf. *borealis* var. *lanceolata*, and *H.* cf. *amphioxys*. Aerophilic taxa are often found where desiccation and freezing are common conditions, including in Antarctica (Spaulding & McKnight 1999), but they are also common in long-distance dust transport (Harper 1999).

The source of the diatoms preserved in this record may be from the local environment surrounding the glaciers. Exposed soil is common on the puna, especially as vegetation becomes sparser with elevation (Kuentz et al. 2011). Nearby ephemeral meltwater ponds that may form during the warm season can also provide a habitat for the diatoms. Furthermore, *bofedales* are common on the slopes of Nevado Coropuna, Quelccaya, and Nevado Sajama (Kuentz et al. 2011, Reese et al. 2013, Phillips et al. 2016). The ecological affinities of the major taxa, which are found in moist soils, wetlands, and other subaerial environments, suggest that these wetland habitats may be the source regions for the diatoms. The valves are well preserved, with some fragmentation, a possible indication of local origin (Fritz et al. 2015). Diatoms, mostly *Muelleria* and *Diadesmis*, that probably dispersed from the surrounding region, where they are selected for by local pressures, have been found in cryoconite holes from Taylor Valley, Antarctica (Stanish et al. 2013). If the diatoms in the ice cores are from the surrounding area, local environments could explain the differences and similarities between the sites.

Long-distance transport of particulate matter is well documented in ice cores elsewhere (Harper 1999), and *H.* cf. *amphioxys* and *P.* cf. *borealis* have also been found in ice cores from high-latitude settings (Donarummo et al. 2003, Harper & McKay 2010). *Pinnularia* and *Luticola* are two common genera found in Swedish cryoconite holes (Vinšová et al. 2015). Vinšová and colleagues reported that these genera made up 12% and 5% of their samples, respectively, and *P. borealis* was one of the most common species encountered. The cryoconite samples also were dominated by *Psammothidium* Bukhtiyarova & Round, *Nitzschia* Hassall, and *Gomphonema* Ehrenberg, all of which were absent or rare in our samples. Their cryoconite communities differed greatly from the surrounding lakes, and possibly originated from farther away. Van de Vijver et al. (2010) also found that cryoconite diatom communities differed from their surrounding water bodies.

Two distinct atmospheric circulation patterns (based on atmospheric pressure) have been identified in the Altiplano (Vuille, 1999; Thompson et al., 2013). The lower 850-hPa

wind advances from the east to the west over the Amazon Basin and is then deflected via topography to the southeast. The higher 500-hPa wind advances from the east and southeast, passing over the mountains. Thompson et al. (2013) analysed major ions in ice cores from Quelccaya, Illimani, and Huascaran. They found that ammonium (NH_4^+) and nitrate (NO_3^-) concentrations in the Quelccaya core correlated with precipitation from the southwest Amazon Basin, brought in on the 850-hPa winds. However, the NO_3^- in the Huascaran core (6050 m a.s.l.), and the NH_4^+ in the Illimani core (6300 m a.s.l.), show an opposite trend relative to Quelccaya. The latter two sites are located under the 500 hPa level. One possible explanation for the differences between the three sites in this study is the elevation of the glaciers. Sajama and Coropuna, like Huascaran and Illimani, are located at higher elevations (6542 and 6450 m a.s.l., respectively), whereas Quelccaya sits ∼ 800 m below at 5670 m a.s.l. Coropuna and Sajama have more taxa in common than either do with Quelccaya. It is possible that the diatoms in Coropuna and Sajama are transported from the east and southeast, and Quelccaya's are originating from the north.

In addition to species composition, the samples from Coropuna and Sajama contain the highest concentration of diatoms, while the Quelccaya samples contained consistently lower amounts (always < 40 valves). Coropuna and Sajama both have high abundances around AD 1800, 262, and 164 valves, respectively. Moreover, at this time, both sites also share similar species compositions, mainly *Pinnularia* spp., *P. borealis*, and *Fragilaria* spp. If the diatoms are the product of long-distance transportation, the coincidence of these high abundances provides some support for these two high-elevation sites having different source areas than Quelccaya. However, it must be noted that the Sajama sample dated to AD ∼ 1764 also has high abundances, but the Coropuna sample from that date does not. Furthermore, wind patterns may not be the only long-distance variable that can explain the similarities and differences between the sites. It is possible that these communities are influenced by both local and long-distance deposition, and that this varies spatially and temporally.

In order to determine the possible origin of the diatoms deposited on the glaciers, diatoms from the surrounding areas, including the wetlands and lakes, need to be studied and quantified. Additional studies on the phytoliths and other particulate matter may also illuminate the processes at work in these cores. Given the rarity and cosmopolitan nature of our species, the diatoms could have originated either from a long-distance global dust source or a local or regional source, complicating their use for reconstructing climate and environment.

Conclusions

The diatoms presented here come from ice cores taken from Nevado Sajama, Nevado Coropuna, and Quelccaya Summit in the tropical Andes. Both freshwater and aerophilic species were found, and most of the species are cosmopolitan, with many being found on several continents. The sites are dominated by subaerial and aerophilic diatoms that are often associated with long-distance aeolian transport (Harper 1999, Donarummo et al. 2003). However, these species are also found in exposed soils and wetlands, which are common in the puna environments that surround the ice caps. Thus, the species composition does not allow differentiation between local versus long-distance sources. In addition, the rarity of diatoms in the ice samples, and the cosmopolitan nature of the species, restricts the use of diatoms in this setting as proxies for past environmental and climatic conditions.

ORCID

D. Marie Weide http://orcid.org/0000-0001-9456-9457

References

Argollo J. & Mourguiart P. 2000. Late Quaternary climate history of the Bolivian Altiplano. *Quaternary Palaeohydrology of South America* 72: 37–51.

Baied C.A. & Wheeler J.C. 1993. Evolution of high Andean puna ecosystems: environment, climate, and culture change over the last 12,000 years in the Central Andes. *Mountain Research and Development* 13: 145–156.

Baker P.A., Rigsby C.A., Seltzer G.O., Fritz S.C., Lowenstein T.K., Bacher N.P. & Veliz C. 2001. Tropical climate changes at millennial and orbital timescales on the Bolivian Altiplano. *Nature* 409: 698–701.

Brack A. & Mendiola C. 2000. *Ecología del Perú*. Editorial Bruño, Lima-Perú.

Burckle L., Gayley R., Ram M. & Petit J. 1988. Diatoms in Antarctic ice cores: some implications for the glacial history of Antarctica. *Geology* 16: 326–329.

Condom T., Coudrain A., Dezetter A., Brunstein D., Delclaux F. & Jean-Emmanuel S. 2004. Transient modelling of lacustrine regressions: two case studies

from the Andean Altiplano. *Hydrological Processes* 18: 2395–2408.

DONARUMMO J., RAM M. & STOERMER E.F. 2003. Possible deposit of soil dust from the 1930's U.S. dust bowl identified in Greenland ice. *Geophysical Research Letters* 30: 17.

FINLAY B.J. 2002. Global dispersal of free-living microbial eukaryote species. *Science* 296: 1061–1063.

FRENGUELLI J. 1939. Diatomeas del Lago Titicaca. *Notas Museo La Plata Botanica* 4: 175–196.

FRENGUELLI J. 1941. Diatomeas del Río de la Plata. *Revista del Museo de La Plata Botanica* 2: 213–334.

FRITZ S.C., BRINSON B.E., BILLUPS W. & THOMPSON L.G. 2015. Diatoms at > 5000 meters in the Quelccaya Summit Dome Glacier, Peru. *Arctic, Antarctic, and Alpine Research* 47: 369–374.

GARREAUD R., VUILLE M. & CLEMENT A.C. 2003. The climate of the Altiplano: observed current conditions and mechanisms of past changes. *Late-Quaternary Palaeoclimates of the Southern Tropical Andes and Adjacent Regions* 194: 5–22.

GAYLEY R., RAM M. & STOERMER E. 1989. Seasonal variations in diatom abundance and provenance in Greenland ice. *Journal of Glaciology* 35: 290–292.

HARPER M. 1999. Diatoms as markers of atmospheric transport. In: *The diatoms: applications for the environmental and earth sciences*, pp. 429–435. Cambridge University Press, Cambridge.

HARPER M. & MCKAY R. 2010. Diatoms as markers of atmospheric transport. In: *The diatoms: applications for the environmental and earth sciences*, pp. 552–559. Cambridge University Press, Cambridge.

HERREROS J., MORENO I., TAUPIN J.D., GINOT P., PATRIS N., ANGELIS M.D., LEDRU M.P., DELACHAUX F. & SCHOTTERER U. 2009. Environmental records from temperate glacier ice on Nevado Coropuna saddle, Southern Peru. *Advances in Geosciences* 22: 27–34.

HONG S., BARBANTE C., BOUTRON C., GABRIELLI P., GASPARI V., CESCON P., THOMPSON L., FERRARI C., FRANCOU B. & MAURICE-BOURGOIN L. 2004. Atmospheric heavy metals in tropical South America during the past 22 000 years recorded in a high-altitude ice core from Sajama, Bolivia. *Journal of Environmental Monitoring* 6: 322–326.

KRAMMER K. & LANGE-BERTALOT H. 1986–1991. *Bacillariophyceae*. Gustav Fischer Verlag, Stuttgart.

KUENTZ A., DE MERA A.G., LEDRU M.P. & THOURET J.-C. 2007. Phytogeographical data and modern pollen rain of the puna belt in southern Peru (Nevado Coropuna, Western Cordillera). *Journal of Biogeography* 34: 1762–1776.

KUENTZ A., LEDRU M.-P. & THOURET J.C. 2011. Environmental changes in the highlands of the western Andean Cordillera, southern Peru, during the Holocene. *The Holocene* 22: 1215–1226.

LIU K., REESE C.A. & THOMPSON L.G. 2005. Ice-core pollen record of climatic changes in the central Andes during the last 400 yr. *Quaternary Research* 64: 272–278.

LIU K., REESE C.A. & THOMPSON L.G. 2007. A potential pollen proxy for ENSO derived from the Sajama ice core. *Geophysical Research Letters* 34. doi:10.1029/2006GL 029018

MARTINY J.B.H., BOHANNAN B.J.M., BROWN J.H., COLWELL R.K., FUHRMAN J.A., GREEN J.L., HORNER-DEVINE M.C., KANE M., KRUMINS J.A., KUSKE C.R., MORIN P.J., NAEEM S., OVREAS L., REYSENBACH A.-L., SMITH V.H. & STALEY J.T. 2006. Microbial biogeography: putting microorganisms on the map. *Nature Reviews Microbiology* 4: 102–112.

METZELTIN D. & LANGE-BERTALOT H. 1998. *Tropische diatomeen in Südamerika I: 700 überwiegend wenig bekannte oder neue taxa repräsentativ als elemente der neotropischen flora*. Koeltz Scientific Books, Koenigstein.

METZELTIN D. & LANGE-BERTALOT H. 2007. *Tropical Diatoms, II: special remarks on biogeographic disjunction*. Koeltz Scientific Books, Koenigstein.

METZELTIN D., LANGE-BERTALOT H. & GARCIA-RODRIGUEZ F. 2005. *Diatoms of Uruguay*. Koeltz Scientific Books, Koenigstein.

PATRICK R. & REIMER C. 1966. *The diatoms of the United States (exclusive of Alaska and Hawaii): systematic descriptions of diatoms of the taxonomic orders Fragilariales, Eunotiales, Achnanthales, and Navicuales (family Naviculaceae)*. The Academy of Natural Sciences, Philadelphia, PA.

PHILLIPS F.M., KELLY M.A., HUDSON A.M., STONE J.O.H., SCHAEFER J., MARRERO S.M., FIFIELD L.K., FINKEL R. & LOWELL T. 2016. CRONUS-Earth calibration samples from the Huancané II moraines, Quelccaya Ice Cap, Peru. *Quaternary Geochronology* 31: 220–236.

POKRAS E.M. & MIX A.C. 1985. Eolian evidence for spatial variability of late Quaternary climates in tropical Africa. *Quaternary Research* 24: 137–149.

RACOVITEANU A.E., MANLEY W.F., ARNAUD Y. & WILLIAMS M.W. 2007. Evaluating digital elevation models for glaciologic applications: an example from Nevado Coropuna, Peruvian Andes. *Global and Planetary Change* 59: 110–125.

REESE C.A. & LIU K. 2002. Pollen dispersal and deposition on the Quelccaya Ice Cap, Peru. *Physical Geography* 23: 44–58.

REESE C.A., LIU K.B. & THOMPSON L.G. 2013. An ice-core pollen record showing vegetation response to Late-glacial and Holocene climate changes at Nevado Sajama, Bolivia. *Annals of Glaciology* 54: 183–190.

SPAULDING S., LUBINSKI D. & POTAPOVA M. 2010. Diatoms of the United States.

SPAULDING S. & MCKNIGHT D. 1999. Diatoms as indicators of environmental change in Antarctic freshwaters. In: *The Diatoms: applications for the environmental and earth sciences*, pp. 245–263. Cambridge University Press, Cambridge.

STANISH L.F., BAGSHAW E.A., MCKNIGHT D.M., FOUNTAIN A.G. & TRANTER M. 2013. Environmental factors influencing diatom communities in Antarctic cryoconite holes. *Environmental Research Letters* 8: 045006.

THOMPSON L.G., DAVIS M.E. & MOSLEY-THOMPSON E. 1994. Glacial records of global climate: A 1500-year tropical ice core record of climate. *Human Ecology* 22: 83–95.

THOMPSON L.G., DAVIS M.E., MOSLEY-THOMPSON E., SOWERS T., HENDERSON K.A., ZAGORODNOV V.S., LIN

P.-N., Mikhalenko V.N., Campen R.K. & Bolzan J.F. 1998. A 25,000-year tropical climate history from Bolivian ice cores. *Science* 282: 1858–1864.

Thompson L.G., Mosley-Thompson E., Bolzan J.F. & Koci B.R. 1985. A 1500-year record of tropical precipitation in ice cores from the Quelccaya ice cap, Peru. *Science* 229: 971–973.

Thompson L.G., Mosley-Thompson E., Dansgaard W. & Grootes P.M. 1986. The Little Ice Age as recorded in the stratigraphy of the tropical Quelccaya ice cap. *Science* 234: 361–364.

Thompson L.G., Mosley-Thompson E., Davis M.E., Porter S.E., Kenny D.V. & Lin P.N. 2017. Tropical ice cores document major droughts in the mid-14th and late-18th centuries linked to ENSO variability and societal disruptions. *The Himalayan Cryosphere: Past and Present*, Geological Society of London, Special issue (in press).

Thompson L.G., Mosley-Thompson E., Davis M.E., Zagorodnov V.S., Howat I.M., Mikhalenko V.N. & Lin P.N. 2013. Annually resolved ice core records of tropical climate variability over the past ∼ 1800 Years. *Science* 340: 945–950.

Van de Vijver B., Mataloni G., Stanish L. & Spaulding S.A. 2010. New and interesting species of the genus Muelleria (Bacillariophyta) from the Antarctic region and South Africa. *Phycologia* 49: 22–41.

Van Eaton A.R., Harper M.A. & Wilson C. 2013. High-flying diatoms: widespread dispersal of microorganisms in an explosive volcanic eruption. *Geology* 41: 1187–1190.

Vinšová P., Pinseel E., Kohler T.J., Van de Vijver B., Žárský J.D., Kavan J. & Kopalová K. 2015. Diatoms in cryoconite holes and adjacent proglacial freshwater sediments, Nordenskiöld glacier (Spitsbergen, High Arctic). *Czech Polar Reports* 5: 112–133.

Vuille M. 1999. Atmospheric circulation over the Bolivian Altiplano during dry and wet periods and extreme phases of the Southern Oscillation. *International Journal of Climatology* 19: 1579–1600.

Williams Jr. R.S. & Ferrigno J.G. 1998. *Glaciers of South America*. *Special Paper 1386-I*. United States Geological Survey. 206 pp.

Zagorodnov V., Thompson L., Ginot P. & Mikhalenko V. 2005. Intermediate-depth ice coring of high-altitude and polar glaciers with a lightweight drilling system. *Journal of Glaciology* 51: 491–501.

Zhou J. & Lau K.M. 1998. Does a monsoon climate exist over South America? *Journal of Climate* 11: 1020–1040.