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A multimillion-year-old record of Greenland vegetation and glacial history preserved in sediment beneath 1.4 km of ice at Camp Century

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Understanding the history of the Greenland Ice Sheet (GrIS) is critical for determining its sensitivity to warming and contribution to sea level; however, that history is poorly known before the last interglacial. Most knowledge comes from interpretation of marine sediment, an indirect record of past ice-sheet extent and behavior. Subglacial sediment and rock, retrieved at the base of ice cores, provide terrestrial evidence for GrIS behavior during the Pleistocene. Here, we use multiple methods to determine GrIS history from subglacial sediment at the base of the Camp Century ice core collected in 1966. This material contains a stratigraphic record of glaciation and vegetation in northwestern Greenland spanning the Pleistocene. Enriched stable isotopes of pore-ice suggest precipitation at lower elevations implying ice-sheet absence. Plant macrofossils and biomarkers in the sediment indicate that paleo-ecosystems from previous interglacial periods are preserved beneath the GrIS. Cosmogenic 26Al/10Be and luminescence data bracket the burial of the lower-most sediment between ~3.2 ± 0.4 Ma and >0.7 to 1.4 Ma. In the upper-most sediment, cosmogenic 26Al/10Be data require exposure within the last 1.0 ± 0.1 My. The unique subglacial sedimentary record from Camp Century documents at least two episodes of ice-free, vegetated conditions, each followed by glaciation. The lower sediment derives from an Early Pleistocene GrIS advance. 26Al/10Be ratios in the upper-most sediment match those in subglacial bedrock from central Greenland, suggesting similar ice-cover histories across the GrIS. We conclude that the GrIS persisted through much of the Pleistocene but melted and reformed at least once since 1.1 Ma.

Pleistocene | ice core | Arctic | climate | ice sheet

The history of the Greenland Ice Sheet (GrIS) and the ecosystems that occupied Greenland during ice-free intervals are poorly known before the Last Glacial Maximum and, particularly, prior to the last interglacial. Most evidence is drawn from marine sediments (1–5), geophysical surveys (6), a few terrestrial deposits (7, 8), and ice-core basal materials (9–12). Because well-dated terrestrial sediment archives are lacking, much of GrIS history is based on offshore records that provide only indirect constraints on ice-sheet extent and terrestrial ecosystems. This fragmentary knowledge of Greenland’s climate history limits our understanding of ice-sheet and ecosystem sensitivity to climate warming.

Knowledge of Greenland glacial history and ecosystems is limited for periods older than ~1 Ma, and in most cases, only glaciation more extensive than present can be directly constrained. Ice-raftered debris (IRD) in marine sediment indicates that Greenlandic glaciers reached the ocean possibly as early as 45 Ma (13) but certainly by 7.5 Ma (1). Ice core grew substantially at 3.3 Ma (14) and culminated in an expanded GrIS by 2.7 Ma (1). Cosmogenic isotopic analyses of IRD and other glacial-marine sediment suggest that glacial erosion began stripping the preglacial landscape by 7 Ma and had eroded most shallow regolith by 1.8 to 2.0 Ma (2, 15). Charcoal and organic debris in outwash near the Hiawatha Crater (16) and pollen in marine sediment in Baffin Bay and the Labrador Sea indicates that boreal forests in humid, cool-temperate to sub-Arctic climates during the Late Pliocene transitioned to tundra vegetation in a cold polar climate during the Early Pleistocene (17, 18). Seismic-reflection surveys record multiple GrIS advances to the edge of the continental shelf in Melville Bay after 2.7 Ma (6).

Significance

Understanding Greenland Ice Sheet history is critical for predicting its response to future climate warming and contribution to sea-level rise. We analyzed sediment at the bottom of the Camp Century ice core, collected 120 km from the coast in northwestern Greenland. The sediment, frozen under nearly 1.4 km of ice, contains well-preserved fossil plants and biomolecules sourced from at least two ice-free warm periods in the past few million years. Enriched stable isotopes in pore ice indicate precipitation at lower elevations than present, implying ice-sheet absence. The similarity of cosmogenic isotope ratios in the upper-most sediment to those measured in bedrock near the center of Greenland suggests that the ice sheet melted and re-formed at least once during the past million years.


The authors declare no competing interest.

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Although poorly dated, rare fossil-rich shallow marine and coastal sediments overlying glacial deposits document warm, forested conditions that imply a smaller GrIS for short (<20 ky) periods between ~2.4 and ~1.8 Ma (7, 8).

Ice-sheet behavior is better known for the past million years because of analyses of ice-core basal materials sourced from landscapes covered by the present GrIS (Fig. 1). In central Greenland, silty ice at the base of the Greenland Ice Core Project (GRIP) ice core is as old as 950 or 970 ka (9, 19). In the nearby Greenland Ice Sheet Project 2 (GISP2) ice core, stratigraphic reconstructions and $\delta^{18}$O dating suggest that the deepest ice is older than 200 ka (20, 21). Silty ice in GISP2 preserves material from a preglacial landscape, which suggests persistent, nonerosive ice cover during much of the Pleistocene (11). Cosmogenic $^{26}$Al/$^{10}$Be data from bedrock in western Greenland (22) and beneath the GISP2 ice core (10) require that ice disappeared from central Greenland at least once within the past 1.1 My. Marine sediment records suggest an ice-free and forested southern Greenland during Marine Isotope Stage (MIS) 11 (374 to 424 ka) (3, 4), while DNA studies of Dye-3 basal materials and forested southern Greenland during Marine Isotope Stage 1368 m of glacial ice and 14 m of silty ice (9). Preservation of ice from MIS 5e (119 to 127 ka) in all Greenland deep ice cores (9, 12, 19) within the past 1.1 My. Marine sediment records suggest an ice-free and forested southern Greenland during Marine Isotope Stage 11 (374 to 424 ka) (3, 4), while DNA studies of Dye-3 basal materials and forested southern Greenland during Marine Isotope Stage 1368 m of glacial ice and 14 m of silty ice (9). Preservation of ice from MIS 5e (119 to 127 ka) in all Greenland deep ice cores (9, 12, 19) (25), and coupled climate-ice sheet models (26) all indicate that the GrIS remained largely intact during the last interglacial. Except for Dye-3 and Camp Century, all ice cores have been collected from Greenland’s interior. Less is known about GrIS extent, behavior, and stability near its margins, the portions of the ice sheet that will melt first and contribute the most to sea-level rise under future warming scenarios (27).

The Camp Century ice core, collected from the ice-sheet periphery in northwestern Greenland, recovered 3.44 m of frozen sediment from beneath 1.368 m of glacial ice and 14 m of silty ice (28); this is the thickest subglacial sedimentary archive recovered from a Greenland ice core (Figs. 1B and 24). Collected in 1966, the subglacial sediment was not studied beyond initial reports of sediment provenance (29) and microfossils, including abundant freshwater diatoms and chrysophyte cysts, pollen, and scarce marine fossils (likely windblown), such as diatoms, sponge spicules, and dinoflagellates (30). The basal material remained in frozen storage for decades until it was rediscovered in 2017. Here, we decipher the glacial and ecological history of northwestern Greenland using analytical techniques that were unavailable when this unique sediment archive was retrieved over 50 years ago. We analyze two samples, respectively, from the upper- and lower-most sections of the Camp Century subglacial sediment. We determine the depositional history and characteristics of the sediment using in situ cosmogenic nuclides, infrared-stimulated luminescence (IRSL), geochemistry, optical microscopy, and scanning electron microscopy and energy dispersive X-ray spectroscopy (SEM-EDS) analyses. We infer weathering conditions, paleo-elevation, and paleoclimatic from pore-ice composition, and we characterize the paleoecology from macrofossil vegetation and biomarkers. We find that the Camp Century subglacial sediment preserves a unique, multimillion-year-old record of glaciation and vegetation. These data are consistent with persistent ice cover interrupted by at least two periods of ice-sheet loss and regrowth, once in the Early Pleistocene and another in the past 1.1 My.

**Results**

The Camp Century subglacial sediment includes two distinct units of frozen diamicton separated by an intermediate layer of debris-rich ice (Fig. 24 and SI Appendix, Supplementary Information Text). Permafrost features such as subhorizontal ice lenses are present only in the lower and intermediate unit. The contact between the intermediate ice layer and the upper diamicton is nonconformable and angular. The two samples we analyzed are from the upper (1059-4) and lower (1063-7) diamicton units (Fig. 2 B and C). Both diamictons contain a variety of lithologies, but the mineralogy is primarily quartz with few feldspars and mafic minerals. The lower sample contains a greater percentage of fine sediment (<125 μm) (Fig. 24 and SI Appendix, Fig. S1; SI Appendix includes full description). Pore-ice major ion chemistry and SEM-EDS analysis of grain coatings indicate greater chemical weathering in the lower sample than the upper sample (Fig. 2 D and E and SI Appendix, Fig. S1 and Table S1).

Cosmogenic $^{26}$Al/$^{10}$Be ratios and IRSL confirm that the upper and lower samples have different histories of exposure and burial (Fig. 2F and SI Appendix, Tables S2–S8). In situ $^{10}$Be and $^{26}$Al are produced in quartz during near-surface exposure to cosmic rays and, when buried, radioactively decay at different rates over time. Relatively low $^{10}$Be concentrations and $^{26}$Al/$^{10}$Be ratios less than that expected from surface production (7.3) indicate long burial with limited exposure before or during the burial period (31) (see SI Appendix, Supplementary Information Text for complete details). The $^{26}$Al/$^{10}$Be ratio in the upper sample (4.5 ± 0.3, n = 6, average ± SD, weighted by $^{26}$Al/$^{10}$Be measurement uncertainty) requires exposure within the past 1.0 ± 0.1 My, while

**Fig. 1.** Greenland ice cores and basal materials. (A) Ice core locations (circles) shown with the bedrock topography and ice surface 1,000 m elevation contours (light gray). (B) Ice core glacier ice thickness (to scale) above the bedrock elevation (dark gray line), basal material thickness (exaggerated), and analyses of basal materials (symbols).

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$^{26}\text{Al}/^{10}\text{Be}$ in the lower sample (1.8 ± 0.4, $n = 3$) indicates longer burial but no more than 3.2 ± 0.4 My (Fig. 2F and SI Appendix, Table S8). Multiple feldspar luminescence dating approaches indicate the lower sample was last exposed to sunlight before 0.7 to 1.4 Ma (SI Appendix, Fig. S3 and Tables S9 and S10). The upper sample did not produce meaningful IRSL results because of light exposure during storage and subsampling.

Sediment pore-ice stable isotopes are enriched in both samples, which require precipitation at elevations lower than the present ice-surface elevation at Camp Century (1,890 m above sea level) and imply ice-sheet absence (SI Appendix, Table S11). Pore-ice $\delta^{18}$O values are 5.9‰ to 7.5‰ greater than mean Late Holocene precipitation (−29‰) at Camp Century (23), which can be explained by both lower surface elevation and possibly warmer temperatures than present. For example, removal of the present ice sheet (thickness of 1.382 m) at Camp Century and isostatic adjustment would raise the current bedrock elevation by ~440 m, implying a net surface elevation lowering of ~950 m. Such an elevation change would account for 5.3 ± 1‰ of the enriched $\delta^{18}$O values in the pore ice, assuming a $\delta^{18}$O/altitude effect of 0.6‰/100 m (32). Temperatures ~0.2 °C to ~3 °C warmer than present and/or phase changes within the sediment account for the remaining $\delta^{18}$O enrichment, assuming a $\delta^{18}$O/temperature sensitivity of 0.7 ± 0.1‰/°C (23) (SI Appendix includes full details). The deuterium excess and $\delta^{13}$O excess values are consistent with modern precipitation and do not indicate alteration (SI Appendix, Table S11).

Terrestrial plant macrofossils are abundant in both samples and preserve a record of the vegetation that occupied northwestern Greenland during ice-free intervals (Fig. 3 A–J and SI Appendix, Figs. S4–S7). The upper sample includes twigs (possibly including Empetrum), moss leaves and stems of Tomentypnum nitens and Polytrichum juniperinum, and sclerotia of the fungus Cenococcum geophilum (Fig. 3 A–H and SI Appendix,
Figs. S4–S6), which are consistent with a tundra ecosystem but could coexist with boreal forest (9). In the lower sample, macrofossils such as bryophyte stems are present (Fig. 3 I and J and SI Appendix, Fig. S7) but not as well preserved and thus difficult to identify. Mixed woody tissue from the upper and lower samples yield δ¹³C ratios of −26.7 ± 0.1‰ and −29.6 ± 0.1‰, δ¹⁵N ratios of 2.4 ± 0.8‰ and −2.3 ± 0.8‰, and C/N ratios ranging from 15.0 to 23.0 and 47.4 to 53.5, respectively, which are consistent with tundra as well as boreal vegetation (SI Appendix, Table S12) (33). A twig from the upper sample yielded a radiocarbon age >50 14C ka (SI Appendix, Table S13).

Well-preserved leaf waxes in Camp Century basal sediment resemble those of modern Greenland tundra ecosystems. Concentrations are higher in the upper sample (Fig. 3 K and SI Appendix, Tables S14 and S15). Both samples contain C₂⁰ to C₃₂ n-alkanoic acids with minimal interference from unsaturated compounds and a high even-to-odd chain length index (>3.45), indicating minimal postdepositional alteration. The n-alkanoic acids are dominated by C₂₄, similar to modern lake sediments in Greenland and soils in the boreal forest regions of Canada (34, 35). The midchain n-alkanes (C₂₁ to C₂₅) have a low odd-to-even chain length index (≤1.0) and coelute with an unidentified complex mixture, likely derived from hydrocarbon-based drilling fluid (SI Appendix, Fig. S8). Long-chain n-alkanes (C₂₇ to C₃₃) have a high odd-to-even chain length index (>4.5) and are dominated by C₂₇ and C₂₉, similar to modern shrubs in Greenland (36).

**Discussion**

The Camp Century subglacial sediment provides a unique stratigraphic record of ice-free ecosystems and ice cover in Greenland. Plant macrofossils and lipid biomarkers in both samples are direct evidence for the preservation of terrestrial paleo-ecosystems beneath the ice sheet. The greatly enriched δ¹⁸O of pore ice in both samples requires that precipitation fell at much lower elevations, demonstrating ice-sheet absence and possibly a warmer climate.
and/or water phase changes in the sediment. Based on differences in stratigraphy, weathering, $^{26}$Al/$^{10}$Be ratios between the upper and lower sediment, and the lower diamicton IRSL minimum burial age (>0.7 to 1.4 Ma), this sedimentary sequence represents at least two episodes of subaerial exposure and subsequent burial. Abundant subhorizontal ice lenses are present only in the lower diamicton, which suggests an active permafrost environment before the emplacement of the upper diamicton unit. The non-conformable contact between the intermediate debris-rich ice layer and the overlying upper diamicton suggests a second glacial advance that incorporated and transported sediment and vegetation from a younger ice-free event.

The Camp Century lower diamicton, buried after 3.2 ± 0.4 Ma ($^{26}$Al/$^{10}$Be maximum age) but before 0.7 to 1.4 Ma (IRSL minimum age), may derive from the growth of the GrIS during the Early Pleistocene (Fig. 4). The cosmogenic $^{26}$Al/$^{10}$Be limiting burial ages fit with the timing of GrIS expansion to the edge of the continental shelf at ~2.7 Ma (Fig. 4E) (1, 6). The presence of extensive grain coatings and high solute concentrations in pore ice are remnants of a weathered surface landscape (2, 15) (Fig. 2). Given the burial age range, macrofossils and lipid biomarkers in the lower diamicton add to growing evidence that paleo-ecosystems from the Early Pleistocene, and perhaps earlier, are preserved both in present ice-free areas (7, 8) as well as below the GrIS (16). The lower diamicton represents the oldest terrestrial record for an ice-free ecosystem recovered beneath the GrIS.

Exposure of the Camp Century upper diamicton within the last 1.0 ± 0.1 My is consistent with paleoclimate records, including basal materials in other ice cores, which suggest a smaller or possibly absent GrIS within the last ~1 My. Ice absence in the northwestern GrIS periphery at Camp Century since 1.0 ± 0.1 Ma agrees with the timing of bedrock exposure below the GrIS summit (<1.1 Ma) (10), which together mandate that much of Greenland was ice free within the last 1.1 My (Fig. 4G and SI Appendix, Table S16). The maximum burial duration for the GISP2 bedrock and the Camp Century upper diamicton are consistent with GRIP basal ice ages (950 to 970 ka) (9, 19). These age constraints require that the GrIS was smaller during the last 1.1 My, most likely during a Pleistocene superinterglacial; however, the precise timing and extent remains uncertain. During MIS 31 (1.06 to 1.09 Ma), global mean sea level reached its Pleistocene maximum (37), and paleotemperatures in northeastern Siberia were elevated (38), consistent with a greatly reduced GrIS (Fig. 4A–C). A smaller-than-present GrIS during the long MIS 11 (374 to 424 ka) interglacial is also possible, as offshore records suggest a more ice-free and forested southern Greenland during this time (3, 4, 9) and sea-level records require significant reduction of the GrIS (39). In contrast, ice-core and geologic evidence (9, 12, 19–21, 23–25) along with modeling studies (26) suggest that the GrIS was mostly intact during MIS 5e (119 to 125 ka).

The similarity of $^{26}$Al/$^{10}$Be burial histories between the Camp Century upper diamicton and GISP2 subglacial bedrock (10) suggests a similar history of ice cover and absence between the GrIS margin and interior (SI Appendix, Fig. S9 and Table S16). The slightly higher $^{26}$Al/$^{10}$Be (4.5 ± 0.3) in the Camp Century upper diamicton than GISP2 bedrock (4.1 to 4.2), and thus slightly shorter burial duration, is consistent with the ice-marginal position of Camp Century. Nevertheless, the similarity not only indicates GrIS presence for much of the Pleistocene but also suggests at least one episode of greatly reduced ice-sheet extent, likely in response to prolonged interglacial warmth. For much of the Pleistocene, the GrIS persisted through interglacial periods while other northern hemisphere ice sheets vanished; however, our data show that the GrIS disappeared from Camp Century at some

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Fig. 4. Paleoclimate and Greenland ice-core age constraints since 4 Ma. (A) Global mean sea level; the dashed black line marks the present (37). (B) Pleistocene superinterglacials since 1.1 Ma (pink columns). (C) Si/Al paleotemperature proxy from Lake El’gygytgyn, Siberia (38). (D) Total minus bisaccate pollen concentration counts in Ocean Drilling Program Site 646, Labrador Sea (3). (E) Changes in GrIS behavior in Melville Bay, west Greenland (6); (F) Green boxes: fossiliferous deposits; KK, Kap København; SK, Store Koldeway (7, 8). (G) Age constraints on materials from Camp Century and other Greenland ice cores (9, 10, 12, 20, 23). The dashed gray line shows bounding age constraints for the Camp Century subglacial sediment.

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point in the last 1.1 My. The Pleistocene resilience of the GrIS and its ability to melt beyond some warming threshold is important information for assessing the risk of sea-level rise under future climatic conditions.

Analysis of the basal silty ice and the remaining archive of subglacial sediment from Camp Century will further resolve the cryostratigraphy, how sediments were emplaced, and the sensitivity of the northwestern GrIS margin to past warming and the types of ecosystems that develop under warmer, ice-free conditions in Greenland. Precise age control of past ice-free episodes recorded in ice-core basal materials, from both existing archives and future drilling campaigns, is key to identifying the climate thresholds that permitted GrIS collapse in the past and, thus, under future warming scenarios.

Materials and Methods

Materials. The subglacial sediment from the Camp Century ice core was collected in 1966 (28). The sediment was stored frozen, initially at University at Buffalo from 1966, until it was transferred to Niels Bohr Institute (NBI) in 1994 and 1996. The samples are kept at ~30 °C as a 10 cm thick subsamples stored in individual glass jars. In the summer of 2019, two samples (1059-4 and 1063-7) were cut at NBI using a dedicated cold-room–hosted diamond-wire saw designed for cutting heterogeneous material (40). Loose material from 1059-4 was kept as a replicate sample (1059-4 Debris).

Sedimentological Description. Basal sediment was inventoried, photographed, and described in October 2019 in the NBI freezer. The dimensions and masses of each subsample were measured to determine the bulk density (~5% uncertainty). We refined the preliminary characterization of the subglacial sediment (29) by describing the granulometry, texture, clast shape, and presence of particular structures, such as ice lenses or deformation features. Our observations and the presence of mixed lithologies indicate that these Camp Century sediments are probably glacial diamictons consisting of glacial and/or periglacial sediments reworked by subsequent ice advances after initial deposition. A full sediment description is in SI Appendix.

Sample Processing. Sample material was sent frozen to the University of Vermont (UVM). We subsampled frozen fragments of original samples for IRSL and SEM-EDS. Samples were thawed at 4 °C inside sample bags. Pore-ice meltwater was decanted from sample bags directly into 50 mL plastic vials. The remaining sediment was transferred into clean, unused plastic bottles and centrifuged, and then meltwater was pipetted into 50 mL plastic centrifuge tubes. Pore-ice melt samples were stored in 50 mL test tubes, capped, sealed, and refrigerated at 4 °C.

Sample drying was carried out at 65 °C, photographed, assigned a soil color, and measured for mass. Sediment was wet sieved with deionized water into ~125, 125 to 250, 250 to 500, 500 to 850, 850 to 2,000, and >2,000 μm grain size fractions. During wet sieving, woody tissue and macrofossils were isolated using a dedicated disposable pipette, dried on a paper filter over a vacuum, and stored frozen. The 250 to 500 and 500 to 850 μm fractions were density separated using lithium polytungstate to isolate the felsic mineral fraction (~2.5 g/cm³).

Major Ion Chemistry. Pore-ice meltwater was aliquoted by volume (1059-4: 4 mL; 1063-7: 0.5 mL) and massed. The samples were diluted to 10 mL (1059-4) and 8 mL (1063-7), remastered, transferred to 10 mL syringes, and filtered through 0.45 μm nylon filters back into the initial vials. Major cations and anions were measured using atomic absorption spectroscopy (PerkinElmer Analyst 300) and 8 mL (1063-7), remassed, transferred to 10 mL syringes, and filtered with a 0.45 μm nylon filters back into the initial vials.

SEM-EDS Analyses of Grain Coatings. Thawed sample materials (~100 mg) were sprinkled on clean paper and embedded in epoxy (EPO-TEK 301). Epoxy plugs were polished using a decreasing grit size to 1 μm and carbon-sputter-coated prior to analysis in backscattered electron mode using a TESCAN VEGA3 scanning electron microscope coupled with an Oxford Instruments AZtec Elemental Mapping EDS in the Geology Department at Middlebury College. EDS maps were acquired at 20 keV for a minimum of 3 min and tricolor plots generated using the Gatan digital micrograph 3.1 software.

Cosmogenic 10Be and 26Al. Quartz purification and beryllium and aluminum extraction were performed independently at UVM (250 to 500 μm and 500 to 850 μm) and Lamont-Doherty Earth Observatory (LDEO), Columbia University (>2,000 μm). At UVM, quartz from the felsic separates of the 250 to 500 and 500 to 850 μm fractions was purified using acid etches (41), and then Be and Al were isolated and extracted using standard procedures (42) specialized for low-concentration samples (43). Two procedural blanks were prepared with the samples during extraction to estimate 10Be and 26Al backgrounds from laboratory sample processing and accelerator mass spectrometry analysis. At LDEO, the >2,000 μm samples were crushed, and quartz was isolated and mostly separated from feldspar by froth flotation. The quartz fraction was subsequently leached in 1% HF/3% HNO3 on a shaker table. Be and Al were isolated and extracted using LDEO procedures (10, 44) for low-level concentrations. The 10Be/26Al ratios in all samples and blanks were measured at the Center for Accelerator Mass Spectrometry, Lawrence Livermore National Laboratory (LLNL), and normalized to primary standard 07KNSTD3110 (assumed 10Be/26Al ratio: 2.850 × 10−15) (SI Appendix, Table S2) (45). At UVM, four blanks (~240 μg 26Al) are included in the in situ blank correction: two processed side by side with samples in this project and two from another batch of low-concentration samples from a separate project processed in the same hood and analyzed together at LLNL. For samples prepared at UVM, we used an average blank 10Be/26Al ratio of 7.4 ± 2.4 × 10−15; we subtracted this ratio from the sample ratios, and propagated uncertainties in quadrature (SI Appendix, Table S3). At LDEO, four blanks (~182 μg 26Al) are included, yielding an average 10Be/26Al ratio of 4.1 ± 1.9 × 10−15 (SI Appendix, Table S4). Blank subtraction and error propagation were calculated using the UVM procedure.
Organic Geochemistry. Bulk woody tissue was analyzed for in silicone oil (56). No pollen was found. Macrofossils were better preserved and more easily dissected with an in-house reference waters previously calibrated against Copenhagen Standard Mean Ocean Water and Standard Light Antarctic Precipitation, using Greenland Ice Sheet Precipitation as a quality standard. The reference waters used were Seattle water and Vostok water, with WW (West Antarctic Greenland Ice Sheet Precipitation) as a quality standard. Mean Ocean Water and Standard Light Antarctic Precipitation, using in-house reference waters previously calibrated against Vienna Standard Mean Ocean Water (VSMOW). The reference water was prepared by LLNL under contract DE-AC52-07NA27344 and LNLJRN-L11066 (A.H.J.).

Data Availability. All study data are included in the article and/or SI.Appendix.

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Lipid Biomarkers. We extracted, purified, and analyzed the n-alkanoic acids and n-alkanes from the <125 μm fraction in the University at Buffalo Organic Stable Isotope Biogeochemistry Laboratory following published procedures (59). We extracted free lipids from homogenized, dried samples on an Accelerated Solvent Extractor (Dionex ASE-200) using methylene chloride (DCM) : methanol 9:1 (volume : volume), flushed three times at 10 min each. We added di-tert-eicosanoic acid and hexatriacontane internal standards to each sample and purified the samples using flash column chromatography. We methylated the acid fraction with diazomethane at 60 °C for 8 h. We quantified the resulting fatty acid methyl ester (FAME) peak areas on a Thermo Trace 1310 Gas Chromatograph with flame ionization detector. We converted peak areas to compound mass by comparison with an external calibration curve established for a C19 FAME standard (for FAMEs) and a C27 alkane standard (for alkanes) and normalized compound mass by dry mass of the extracted sediment.

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