



Plant, insect, and fungi fossils under the center of Greenland's ice sheet are evidence of ice-free times

Paul R. Bierman^{a,1}, Halley M. Mastro^a, Dorothy M. Peteet^{b,c}, Lee B. Corbett^a, Eric J. Steig^d, Chris T. Halsted^e, Marc M. Caffee^f, Alan J. Hidy^g, Greg Balco^g, Ole Bennike^h, and Barry Rockⁱ

Edited by Eric Rignot, University of California Irvine, Irvine, CA; received May 9, 2024; accepted June 17, 2024

The persistence and size of the Greenland Ice Sheet (GrIS) through the Pleistocene is uncertain. This is important because reconstructing changes in the GrIS determines its contribution to sea level rise during prior warm climate periods and informs future projections. To understand better the history of Greenland's ice, we analyzed glacial till collected in 1993 from below 3 km of ice at Summit, Greenland. The till contains plant fragments, wood, insect parts, fungi, and cosmogenic nuclides showing that the bed of the GrIS at Summit is a long-lived, stable land surface preserving a record of deposition, exposure, and interglacial ecosystems. Knowing that central Greenland was tundra-covered during the Pleistocene informs the understanding of Arctic biosphere response to deglaciation.

cosmogenic | interglacial | paleoclimate | paleobotany

Although marine sediment provides information about long-term Greenland Ice Sheet (GrIS) history (1), terrestrial materials older than about 21 ka are scarce (2). Thus, the information needed to reconstruct the size of the GrIS over time is lacking. Analysis of marine sediment reveals the distribution of terrestrial ecosystems during interglacials, but it cannot provide high spatial resolution (3). In contrast, materials collected from below the GrIS record location-specific ice extent and climate, providing direct evidence for past ice sheet absence and biosphere response. For example, data from the 1966 Camp Century (CC) core in northwest Greenland elucidate retreat timing, glacial processes, and former tundra ecosystems within 150 km of the ice margin (4, 5). Because there is a wide range of ice-extent scenarios under which CC could be ice-free, that core provides little information about central Greenland, the thickest and largest part of the ice sheet, which dominates GrIS contributions to global sea level (Fig. 1*A*).

In 1993, the Greenland Ice Sheet Project 2 (GISP2) recovered the only basal material from central Greenland: 40 cm of erratic boulders, 8 cm of till, and 105 cm of rock (Fig. 1*B*) 6–8. Analysis of sediment in the lowest basal ice revealed substantial organic carbon and nitrogen and meteoric ¹⁰Be—consistent with limited erosion, long subaerial exposure, and the presence of soil (9). A depth profile of cosmogenic nuclides from the GISP2 subglacial rock core indicated that central Greenland deglaciated at least once in the last 1.1 My (6). Here, we re-examine the till to learn about past conditions at Summit.

Results

Purified quartz, isolated from sand in the till, had $32,820 \pm 2,780$ atoms g⁻¹¹⁰Be, 91,150 \pm 18,290 g⁻¹²⁶Al, and ²⁶Al/¹⁰Be of 2.8 \pm 0.6, indicative of no more than 2.0 \pm 0.4 million years of burial after the last substantive near-surface exposure (Fig. 1*D*). When sieving the sediment (Fig. 2*A*), we found vegetation fragments (Fig. 2*B*) including a bud scale of *Salix* sp. (willow) and 129 megaspores of *Selaginella rupestris* (rock spike-moss) with interwoven reticulation. Some megaspores had a visible trilete scar (y-shaped suture) on the surface and others did not, a phenomenon common in *S. rupestris* (10). We also found a *Papaver* sect. *Scapiflora* (poppy) seed, 155 sclerotia of the soil fungus *Cenococcum geophilum*, and the remains of an insect leg and compound eye. We isolated seven pieces of angiosperm wood. In three wood samples, scanning electron microscopy showed vessel elements with simple perforation plates and large simple lateral wall pitting indicative of *Salix*. Helical wall thickenings suggest that this wood was from immature plants.

Discussion

The presence of poppy, spike-moss, fungal sclerotia, woody tissue, and insect parts in the GISP2 till shows that tundra vegetation once covered central Greenland, mandating that the island was largely ice-free. The fossil assemblage suggests that ice was replaced by a cold, dry, open environment where snow lingered into summer. We make this interpretation

Author affiliations: ^aRubenstein School of Environment and Natural Resources, University of Vermont, Burlington, VT 05405; ^bNASA/Goddard Institute for Space Studies, New York, NY 10025; ^cLamont Doherty Earth Observatory, Palisades, NY 10964; ^dEarth and Space Sciences, University of Washington, Seattle, WA 98195; ^cDepartment of Geosciences, Williams College, Williamstown, MA 01267; ^fDepartment of Physics and Astronomy, Purdue University, West Lafayette, IN 47907; ^aLawrence Livermore National Laboratory, Livermore, CA 94550; ^hGeological Survey of Denmark and Greenland, Copenhagen DK-1350, Denmark; and 'Natural Resources and the Environment, University of New Hampshire, Durham, NH 03824

Author contributions: P.R.B. and H.M.M. designed research; P.R.B., H.M.M., D.M.P., L.B.C., E.J.S., C.T.H., M.M.C., A.J.H., G.B., O.B., and B.R. performed research; C.T.H., M.M.C., A.J.H., and G.B. contributed new reagents/ analytic tools; P.R.B., H.M.M., D.M.P., L.B.C., E.J.S., C.T.H., M.M.C., A.J.H., G.B., O.B., and B.R. analyzed data; and P.R.B., H.M.M., D.M.P., L.B.C., E.J.S., C.T.H., M.M.C., A.J.H., G.B., O.B., and B.R. wrote the paper.

The authors declare no competing interest.

Copyright © 2024 the Author(s). Published by PNAS. This open access article is distributed under Creative Commons Attribution-NonCommercial-NoDerivatives License 4.0 (CC BY-NC-ND).

Although PNAS asks authors to adhere to United Nations naming conventions for maps (https://www.un.org/ geospatial/mapsgeo), our policy is to publish maps as provided by the authors.

 ^1To whom correspondence may be addressed. Email: pbierman@uvm.edu.

This article contains supporting information online at https://www.pnas.org/lookup/suppl/doi:10.1073/pnas. 2407465121/-/DCSupplemental.

Published August 5, 2024.



Fig. 1. Map, sample, and isotopic data. (*A*) Map of coring sites. (*B*) Subglacial core collected at GISP2 showing numbered sections analyzed for cosmogenic nuclides (6) and till (this study). (*C*) Isotope data including both rock data (6) and till (this study). (*D*) Two isotope plot indicating difference in sand-size quartz grains from GISP2 (6, this study) and CC (4). B and C modified from ref 6; base image for C provided by U.S. National Science Foundation Ice Core Facility.

because we found *S. rupestris*, which forms creeping mats on sandy gravel or rocky places (11) and is today found only in southern Greenland (12). *S. rupestris* forms spores, such as those identified in the till, during late July (13). *Papaver* sect. *Scapiflora* is a dominant member of the most depauperate vegetation assemblage that borders the Arctic Ocean. In the High Arctic, they grow in areas with long-lasting snow cover (14). *Papaver* blooms in June–July and is pollinated by bees in early summer but by flies later (15).

The very dry exposed vegetation assemblage with abundant *S. rupestris* megaspores, fragile *Cenococcum* fungal sclerotia, and lack of other taxa including bryophytes suggests minimal fossil transport and a mean July temperature in central Greenland somewhere between 1 and 10 °C (16) reflecting the wide distribution of *Papaver* sect. *Scapiflora* today in Greenland (17). The botanically determined temperature range is consistent with the 3 to 7 °C range derived using lapse rates (*SI Appendix*). The abundance of macrofossils in the till explains the organic carbon and nitrogen found in sediment from GISP2 basal ice. High concentrations of meteoric ¹⁰Be (9) on basal ice sediment reflect stability and exposure of the soil developed on the till in which the plants grew.

Cosmogenic nuclide analysis of the sand from till fills an important gap in the ¹⁰Be and ²⁶Al stratigraphy of the GISP2 subglacial core (Fig. 1*C*). The congruent depth profile of ¹⁰Be at GISP2 indicates that the erratic, the till, and the rock below were likely exposed together under a shallow (meters thick) cover of sediment or ice (6). If true, this requires till and erratic deposition prior to near-surface exposure of the cored material, minimal erosion since exposure, and at least one period of deglaciation.

The timing of the most recent exposure of Summit remains uncertain although rock core ${}^{26}\text{Al}/{}^{10}\text{Be}$ data indicate that it occurred within the last 1.1 My (6). Argon measurements in the overlying clear ice suggest that it persisted for at least the past 250 ky (18). Some basal ice at the Greenland Ice Core Project 30 km away (Fig. 1*A*) is about 1 My old (19). Luminescence dating of the existing GISP2 till sample is not possible because the till was melted and exposed to light after coring, unlike the frozen fluvial sediment at Camp Century (4). Even if the sample had been stored in darkness, till, because it is deposited under ice, is not typically useful for dating surface exposure with luminescence. However, mass movements, which are common when permafrost thaws, could have exposed the till after deglaciation and incorporated the macrofossils. The young *Salix* wood supports such instability and soil stirring.

Excellent preservation of the fossils makes it unlikely that they lived during a prior interglacial and were incorporated in the till as ice readvanced over central Greenland. Surface instability would also explain the 40 cm of erratic boulders sitting over the fossil-rich soil developed on the thin till. In any case, the fossil ecosystem at GISP2 supports the assertion (6, 20) that Greenland's ice sheet was not an entirely stable feature of the Pleistocene Arctic.



Fig. 2. GISP2 till and macrofossils found in it: (*A*) Photo of the angular-clast-rich till section of the GISP2 subglacial core, taken 1994, up core to left (Credit: T. Gow, supplied by D. Meese). (*B*) Overview of sediment, mostly quartz and fossils. (*C*) Wood fragment. (*D*) Vertical orientation typical of GISP2 wood. (*E*) Wood at higher magnification showing simple pits in lateral vessel wall (1) and distinct simple perforation plate (2), along with the helical thickening typical of GISP2 wood. (*F*) Bud scale of *Salix* (willow). (*G*) Sclerotium of the soil fungus *C. geophilum** (*H*) Insect eye, possibly from a fly*. (*J*) *S. rupestris* megaspore. (*J*) Seed of *Papaver* sect. *Scapiflora*. The asterisk shows macrofossil types also found in Camp Century sediment by ref. 5. Wood fragment images are same specimen.

The presence of plant and insect macrofossils, now documented closer to the margin (CC) and at the center (GISP2) of the GrIS, suggests that recovery of basal ice, sediment, and underlying rock from central and eastern locations in Greenland is a high priority. Analysis of these materials will refine the understanding of ice and biosphere response during past warm periods, imperfect but important analogs for human-induced climate warming. Critical to the quest for subglacial archives will be drilling locations where the ice has remained frozen to the bed, and thus nonerosive, preserving sediment and fossils from past warm periods when the ice was gone.

- 1. H. C. Larsen et al., Seven million years of glaciation in Greenland. Science 264, 952-955 (1994).
- K. H. Kjær et al., A 2-million-year-old ecosystem in Greenland uncovered by environmental DNA. Nature 612, 283–291 (2022).
- A. De Vernal, C. Hillaire-Marcel, Natural variability of Greenland climate, vegetation, and ice volume during the past million years. *Science* 320, 1622–1625 (2008).
- A. J. Christ et al., Deglaciation of northwestern Greenland during Marine Isotope Stage 11. Science 381, 330–335 (2023).
- A. J. Christ et al., A multimillion-year-old record of Greenland vegetation and glacial history preserved in sediment beneath 1.4 km of ice at Camp Century. Proc. Natl. Acad. Sci. U.S.A. 118, e2021442118 (2021).
- J. M. Schaefer et al., Greenland was nearly ice-free for extended periods during the Pleistocene. Nature 540, 252-255 (2016).
- A. J. Gow et al., Physical and structural properties of the Greenland Ice Sheet Project 2 ice core: A review. J. Geophys. Res. 102, 26559–26575 (1997).
- A. J. Gow, D. A. Meese, Nature of basal debris in the GISP2 and Byrd ice cores and its relevance to bed processes. Ann. Glaciol. 22, 134–140 (1996).
- P. R. Bierman et al., Preservation of a preglacial landscape under the center of the Greenland Ice Sheet. Science 344, 402–405 (2014).
- P. Korall, W. A. Taylor, Megaspore morphology in the Selaginellaceae in a phylogenetic context: A study of the megaspore surface and wall structure using scanning electron microscopy. Grana 45, 22–60 (2006).

Materials and Methods

We isolated fossils and purified quartz from the sand fraction of the till before extracting ¹⁰Be and ²⁶Al. We identified fossils using reference collections and electron microscopy. Detailed methods are provided in *SI Appendix*.

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

ACKNOWLEDGMENTS. Supported by NSF-2114629, -1735676, -2300560, and -2114631 and the Ice Core Facility (-2041950). We thank A. Christ for sample processing. Lawrence Livermore National Laboratory part of this work conducted under Contract DE-AC52-07NA27344 as LLNL-JRNL-861062.

- A. E. Porsild, W. J. Cody, Vascular Plants of Continental Northwest Territories, Canada (National Museum of Natural Sciences, National Museums of Canada, 1980).
- J. Feilberg, A phytogeographical study of South Greenland. Vascular plants. *Meddelelser om Grønland. Biosci.* 15, 70 (1984).
- Flora of North America, 4: Magnoliophyta: Caryophyllidae, Part 1 (Oxford University Press, 2003).
- I. Brattbakk, "Flora og vegetasjon" in Svalbardreinen Og Dens Livsgrunnlag, N. A. Øritsland, Ed. (Universitetsforlaget, 1986), pp. 15–34.
- P. Molgaard, Temperature relations of yellow and white flowered Papaver radicatum in North Greenland. Arctic Alpine Res. 21, 83 (1989).
- 16. D. A. Walker et al., The Circumpolar Arctic vegetation map. J. Veg. Sci. 16, 267-282 (2005).
- C. Bay, A Phytogeographical Study of the Vascular Plants of Northern Greenland-North of 74 Northern Latitude (Museum Tusculanum Press, 1992).
- M. L. Bender, E. Burgess, R. B. Alley, B. Barnett, G. D. Clow, On the nature of the dirty ice at the bottom of the GISP2 ice core. *Earth Planet. Sci. Lett.* 299, 466–473 (2010).
- A. M. Yau, M. L. Bender, T. Blunier, J. Jouzel, Setting a chronology for the basal ice at Dye-3 and GRIP: Implications for the long-term stability of the Greenland Ice Sheet. *Earth Planet. Sci. Lett.* 451, 1–9 (2016).
- P. Bierman et al., A persistent and dynamic East Greenland Ice Sheet over the past 7.5 million years. Nature 540, 256–260 (2016).