

Significantly warmer Arctic surface temperatures during the Pliocene indicated by multiple independent proxies

A.P. Ballantyne^{1*}, D.R. Greenwood², J.S. Sinninghe Damsté³, A.Z. Csank⁴, J.J. Eberle¹, and N. Rybczynski⁵

¹Department of Geological Sciences, University of Colorado, Boulder, Colorado 80309, USA

²Department of Biology, Brandon University, Brandon, Manitoba R7A 6A9, Canada

³Department of Marine Organic Biogeochemistry, Royal Netherlands Institute for Sea Research (NIOZ), Texel 1797 SZ, Netherlands

⁴Department of Geosciences and Laboratory of Tree-Ring Research, University of Arizona, Tucson, Arizona 85721, USA

⁵Canadian Museum of Nature, Ottawa, Ontario K1P 6P4, Canada

ABSTRACT

Temperatures in the Arctic have increased by an astounding 1 °C in response to anthropogenic forcing over the past 20 years and are expected to rise further in the coming decades. The Pliocene (2.6–5.3 Ma) is of particular interest as an analog for future warming because global temperatures were significantly warmer than today for a sustained period of time, with continental configurations similar to present. Here, we estimate mean annual temperature (MAT) based upon three independent proxies from an early Pliocene peat deposit in the Canadian High Arctic. Our proxies, including oxygen isotopes and annual ring widths (MAT = -0.5 ± 1.9 °C), coexistence of paleovegetation (MAT = -0.4 ± 4.1 °C), and bacterial tetraether composition in paleosols (MAT = -0.6 ± 5.0 °C), yield estimates that are statistically indistinguishable. The consensus among these proxies suggests that Arctic temperatures were ~19 °C warmer during the Pliocene than at present, while atmospheric CO₂ concentrations were ~390 ppmv. These elevated Arctic Pliocene temperatures result in a greatly reduced and asymmetrical latitudinal temperature gradient that is probably the result of increased poleward heat transport and decreased albedo. These results indicate that Arctic temperatures may be exceedingly sensitive to anthropogenic CO₂ emissions.

INTRODUCTION

Throughout most of the Cenozoic era (0–65.5 Ma), temperatures at Earth's surface have exceeded modern temperatures (Zachos et al., 2008). This is especially true for the Arctic (Dowsett, 2007; Robinson, 2009). The most recent interval in which sustained global temperatures exceeded those of today was during the Pliocene epoch (2.6–5.3 Ma), when global surface temperatures were between 2 and 3 °C warmer than present (Dowsett, 2007). Although tropical surface temperatures during the Pliocene were only slightly warmer than present (Dowsett, 2007), Arctic temperatures were probably much warmer (Robinson, 2009). However, the magnitude of Arctic Pliocene warming remains poorly constrained, primarily because ice core records do not extend this far back. Thus, researchers have had to rely on other proxy records to reconstruct Arctic temperatures during the Pliocene.

Here we use three independent proxies to better constrain terrestrial surface temperatures (TSTs) for the High Arctic during the Pliocene. We use fossil tetraether lipids derived from soil bacteria, oxygen isotope ratios ($\delta^{18}\text{O}$) and annual ring widths in fossil wood, as well as the composition of paleovegetation (see the Appendix) from the Beaver Pond site on Ellesmere Island (78°N, 82°W, and 378 masl; see Fig. DR1 in the

GSA Data Repository¹) to derive independent paleotemperature estimates.

RESULTS AND DISCUSSION

The bacterial tetraether membrane composition in soils has been shown to be very sensitive to environmental conditions (Weijers et al., 2007). In particular, the degree of cyclization and methylation among branched tetraethers is highly dependent upon pH and temperature,

making fossil tetraether lipids an excellent proxy for reconstructing TSTs (Weijers et al., 2007) (see Appendix). The analysis of bacterial tetraether composition in peat collected from the Beaver Pond site indicates a MAT of -0.6 ± 5.0 °C that suggests Pliocene temperatures in the Arctic were considerably warmer than the modern MAT of -19.7 °C at Eureka, Nunavut (Environment Canada, 2009) (79°N, 85°W), yielding a temperature difference (ΔMAT) of ~19 °C (Table 1).

Refined paleotemperature estimates from the annual growth rings and $\delta^{18}\text{O}$ of cellulose in fossil wood also showed considerably warmer TSTs in the Arctic during the Pliocene, yielding a MAT of -0.5 ± 1.9 °C and a ΔMAT of ~19 °C (Table 1). Although a previous estimate based on this approach yielded a MAT of approximately -5 °C, additional information from oxygen isotopes in mosses at the site allowed us to calculate isotopic enrichment in the cellulose of fossil trees, thereby reducing assumptions and increasing the precision of our MAT estimates (see the Data Repository).

It is conceivable that the isotope and tetraether paleotemperature proxies are biased toward the warm season because they are effectively the

TABLE 1. PALEOTEMPERATURE PROXY ESTIMATES FOR THE ARCTIC DURING THE PLIOCENE AND THEIR ASSOCIATED STATISTICS

Temperature proxies	Temperature transfer function	MAT (°C)	ΔMAT (°C)	$\pm\text{SE}$
Tetraethers	$\text{MAT} = (\text{MBT} - 0.122 - 0.187 \times \text{CBT})/0.020$	$-0.6^{\dagger,\S}$	19.1	5.0
Tree ring isotopes	$\text{MAT} = 17.5 + 0.98 \times \delta^{18}\text{O}_{\text{pre}} - 2.71 \times \text{RW}$	$-0.5^{*,\dagger}$	19.2	1.9
Paleovegetation	CLIMST	$-0.4^{*,\S}$	19.3	4.1
Composite	N.A.	-0.4	19.3	0.4

Note: Estimates of mean annual temperature (MAT), difference from modern temperature (ΔMAT), and standard error (SE) for each temperature proxy are reported. We used the CLIMST algorithm based on the coexistence approach (Mosbrugger and Utescher, 1997) to estimate temperature from paleovegetation. Estimates of MAT from the three independent proxies were statistically indistinguishable. The composite estimate is based upon the joint distribution of temperature estimates resampled using a bootstrap technique (Efron and Tibshirani, 1997). CBT—Cyclisation of branched tetraethers; MBT—Methylation of branched tetraethers; pre—precipitation; RW—annual ring-width.

^{*}No statistical difference between distributions of estimates (p-value = 0.79).

[†]No statistical difference between distributions of estimates (p-value = 0.77).

[§]No statistical difference between distributions of estimates (p-value = 0.72).

¹GSA Data Repository item 2010165, supplemental information, is available online at www.geosociety.org/pubs/ft2010.htm, or on request from editing@geosociety.org or Documents Secretary, GSA, P.O. Box 9140, Boulder, CO 80301, USA.

*E-mail: ashley.ballantyne@colorado.edu.

result of summer productivity. Temperature estimates derived from tetraether composition may be more representative of summer processes when temperatures are higher and soils have greater water content, promoting the facultative anaerobic bacteria that are hypothesized to synthesize tetraether lipids (Weijers et al., 2007). However, temperature estimates derived from tetraethers in modern soils from Svalbard, Norway (MAT ≈ -4 °C) were within 2 °C of instrumental temperature records (MAT ≈ -6 °C), suggesting that tetraethers are an effective proxy for reconstructing temperatures from paleosols at high latitudes (Peterse et al., 2009). It is also possible that MAT estimates from isotopes and annual ring widths may be biased toward summer months because this is when trees are accruing biomass and synthesizing cellulose from the available water. Although it is unclear how much of the water pool available for photosynthesis is derived from winter versus summer precipitation, research on oxygen isotopes in modern larch suggests that larch rely on spring snow melt and thus integrate the isotopic signal of annual precipitation (Sugimoto et al., 2002). Furthermore, these two independent proxies effectively yield the same temperature estimate (Table 1), providing greater confidence in our estimates of appreciably warmer temperatures in the Arctic during the Pliocene.

The third temperature proxy we employed at the Beaver Pond site was paleovegetation composition (Table 1). By utilizing a slightly modified coexistence approach (Mosbrugger and Utescher, 1997), we were able to generate climatic ranges for 16 plant genera identified at the site and a MAT estimate (see Appendix). Several genera identified at the Beaver Pond site occur in much warmer climates today, including Northern white cedar (*Thuja occidentalis*) that has a modern distribution with a MAT range of -4.4 to 14.2 °C and Rough Cinquefoil (*Potentilla norvegica*) that has a modern distribution with a MAT range of -5.1 to 14.0 °C (Fig. 1). However, also preserved at this site are cooler-climate taxa such as a dwarf shrub form of Birch (*Betula nana*) (MAT = -13.4 to 3.7 °C). Although a broad range of TSTs was inferred from individual plant taxa present at our site, the coexistence interval among all taxa gives an estimated MAT of -0.4 ± 4.1 °C, yielding a Δ MAT of ~ 19 °C (Table 1). Applying a similar coexistence approach, we also estimated a cold-month mean temperature (CMMT) of -11.6 ± 7.1 °C and a warm-month mean temperature (WMMT) of 14.4 ± 2.0 °C.

Our WMMT estimate of 14.4 ± 2.0 °C compares well with a previous WMMT estimate of 12.4 °C based on the assemblage of fossil beetles from this site (Elias and Matthews, 2002), which is not too surprising given that both methods are based on correspondence

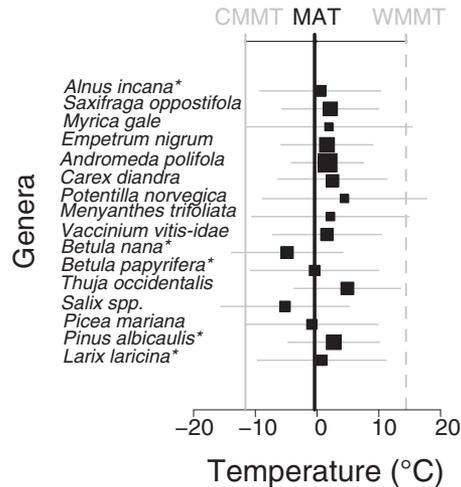


Figure 1. Paleotemperatures for the Pliocene Beaver Pond site inferred from paleovegetation. Plotted are the inferred temperature estimates based on the coexistence approach (Mosbrugger and Utescher, 1997). Black boxes represent mean annual temperature (MAT) estimates for each genus identified at the site, with gray whiskers representing the minimum MAT and maximum MAT of the range for each genus. The area of the box is relative to the precision of the temperature estimate (1/SE). The overall MAT inferred as the mean of the temperature range was -0.4 °C (black line). The overall cold-month mean temperature (CMMT) inferred as the mean across all taxa was -11.6 °C (gray solid line), and the overall warm-month mean temperature (WMMT) inferred as the mean across all taxa was 14.4 °C (gray dashed line). *Salix spp.* refers to *Salix alaxensis* and *Salix arbusculoides* and their combined climatic range. Species noted with an asterisk were selected as best matches for fossils identified to genus only.

with nearest living relatives (Elias and Matthews, 2002; Greenwood and Wing, 1995). However, the paleovegetation-based CMMT of -11.6 ± 7.1 °C is considerably warmer than the CMMT of -26.6 °C derived from the beetle assemblage (Elias and Matthews, 2002). Although beetles and plants are both effectively ectothermic, and thus sensitive indicators of ambient temperature, beetles can better regulate their temperature under cold conditions by physiological mechanisms, such as increased respiration (Morgan and Bartholomew, 1982), and behavioral mechanisms, such as burrowing (Strathdee and Bale, 1998). These mechanisms allow beetles to inhabit colder climates and may explain the anomalously low CMMT indicated by the beetle assemblage. In fact, Elias and Matthews (2002) showed a much better relationship between modern beetle distributions and WMMT ($r^2 = 0.95$) than CMMT ($r^2 = 0.80$), suggesting that the seasonal range of warming inferred from the beetle assemblage (Δ MAT = 10.0 to 14.8 °C) is probably biased low.

CONCLUSIONS

The three independent temperature proxies measured from the same peat deposit converge on an Arctic MAT for the Pliocene of ~ 0 °C that corresponds with a Δ MAT of ~ 19 °C (Table 1). Because these independent proxy estimates of MAT are statistically indistinguishable from each other (Table 1), we combined all of the estimates into a joint distribution that was then resampled using a bootstrap technique (see Appendix). This approach yielded a composite MAT estimate of -0.4 ± 0.4 °C, and a Δ MAT of 19.3 °C (Table 1). This more robust temperature estimate suggests that Arctic temperatures were remarkably warmer during the Pliocene (Fig. 2). In fact, these estimates are 5 – 10 °C warmer than previous proxy estimates (Baltanyne et al., 2006; Elias and Matthews, 2002). These temperature estimates are also considerably warmer than model simulations at high latitudes (Haywood et al., 2009). However, climates at high latitude are known to be very sensitive to orbital parameters affecting insolation (Ravelo et al., 2004), and thus proxy estimates with uncertain age constraints are not directly comparable to model simulations that typically span hundreds of years. Nonetheless, the agreement among these estimates indicates significant Arctic warming during the Pliocene.

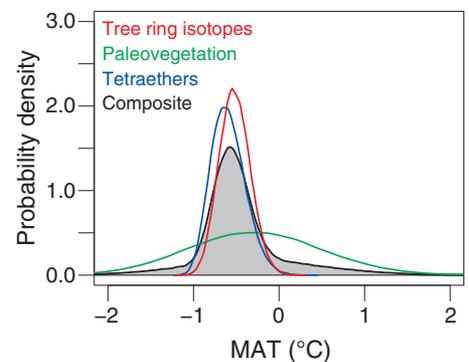


Figure 2. Probability density functions of mean annual temperature (MAT) estimates for the Arctic during the Pliocene based on three independent proxies. Plotted are the three bootstrapped estimates of MAT derived from our three proxies (colored lines) and the density function for the composite estimate of MAT derived from resampling the joint distribution across all three independent proxies (gray filled).

The Pliocene is a paradox when compared to other Cenozoic warm intervals because global mean temperatures were 2 – 3 °C warmer than present (Dowsett, 2007), despite levels of atmospheric CO_2 that were only slightly higher than preindustrial levels (Fedorov et al., 2006). Recent proxy estimates that are better constrained indicate Pliocene atmospheric CO_2

levels of ~390 ppmv (Pagani et al., 2010), which are comparable to today's levels (~385 ppmv). However, if we place our estimates of Pliocene Arctic TSTs in a global context, most of the temperature response to climate forcing is due to increased temperatures at high latitudes. This increased climate sensitivity at high latitudes has resulted in a greatly reduced latitudinal temperature gradient (Fig. 3A). Several mechanisms have been hypothesized to explain this reduced temperature gradient, including increased poleward heat transport, decreased ice albedo, and changes in cloud cover (Fedorov et al., 2006).

Most of the observed decline in the latitudinal temperature gradient during the Pliocene can be explained by increased poleward heat transport. Model experiments suggest that a 15% increase in the poleward transport of sensible heat by ocean circulation is sufficient to explain the reduced latitudinal gradient in sea surface temperatures (SSTs) observed during the Pliocene (Dowsett et al., 1992). Model simulations of the atmosphere also indicate an increase in the poleward transport of latent heat as precipitation, mainly at tropical latitudes (Haywood et al., 2009). However, Earth's surface energy balance dictates that net poleward heat transport should be symmetrical in both hemispheres. According to our temperature estimates, the Arctic was ~19 °C warmer during the Pliocene than today, whereas Antarctica was only ~13 °C warmer

(see Fig. 3B; Table DR2 in the Data Repository), resulting in an "Arctic tail" in the latitudinal temperature distribution (Fig. 3B). This tail is even more pronounced during the Eocene, when temperatures in the Arctic were almost 35 °C warmer than present (Fig. 3B). Therefore, the decreased temperature gradient can be explained in part by increased poleward heat transport, but other physical mechanisms must be invoked to explain the observed asymmetry in the latitudinal temperature gradient.

This pronounced Arctic tail in the latitudinal temperature gradient can be explained in part by a greater ice-albedo feedback in the Arctic compared to Antarctica. Ice has a much higher albedo (~0.7) (Lindsay and Rothrock, 1994) relative to the ocean (~0.07) (Payne, 1972) than it does relative to forest (~0.1–0.4) (Betts and Ball, 1997). Therefore removal of ice from the ocean decreases surface albedo by a factor of ten, compared with removal of ice from the land, which decreases surface albedo by a factor of only two to seven. Given that the northern polar region is dominated by water, whereas the southern polar region is dominated by land, one would expect a greater temperature response to changes in ice extent in the Arctic than Antarctica. However, the exact timing and extent of sea ice formation and continental glaciation in the Arctic during the Pliocene remains uncertain (Zachos et al., 2008). Although there is limited evidence of ice-rafted debris in the Arctic from the Miocene and into the Eocene, suggesting some continental glaciation (Stickley et al., 2009; St. John and Kriesek, 2002), empirical evidence suggests that widespread Northern Hemisphere glaciation did not occur until 2.75 Ma (Ravelo et al., 2004), which is substantiated by recent Pliocene paleotemperature SST estimates near Svalbard between 10 and 18 °C (Robinson, 2009). This is corroborated by model simulations indicating that atmospheric CO₂ levels must fall below 280 ppmv to promote widespread continental glaciation of the Northern Hemisphere (DeConto et al., 2008) and 250 ppmv to promote major continental glaciation on Greenland (Lunt et al., 2008), both of which are well below recent estimates of Pliocene atmospheric CO₂ estimates of ~390 ppmv (Pagani et al., 2010). Our MAT estimates near 0 °C, in combination with well-documented widespread forest ecosystems (Matthews and Ovenden, 1990), provide independent lines of evidence suggesting limited glacial extent in the Arctic during the Pliocene. Thus the differential magnitude of ice-albedo feedbacks between the Arctic and Antarctica may help to explain apparent asymmetries in the latitudinal temperature gradient.

Clouds have also been invoked as a physical mechanism to explain the amplification of Arctic temperatures during warmer Cretaceous periods (Kump and Pollard, 2008). However,

the modeled effects of clouds on Arctic climate are highly dependent upon the physical properties and seasonal distribution of clouds. A recent study by Abbot and Tziperman (2008) shows that deep convective clouds can produce significant winter warming under ice-free conditions. In contrast, reduced summer cloud cover may lead to warmer, more equable climates (Kump and Pollard, 2008). Although these studies clearly illustrate the importance of cloud cover on the radiative balance of the Arctic, variations in the seasonal sign and magnitude of the radiative forcing associated with clouds must be further investigated.

Therefore the reduced temperature gradient can be explained in part by an increase in meridional heat transport by either the oceans or the atmosphere. However, the mechanism of increased poleward heat transport cannot be the only physical mechanism driving the reduced temperature gradient because it is in fact the surface temperature gradient that ultimately drives the flux of heat poleward. Thus other mechanisms such as ice-albedo feedbacks and changes in cloud cover must be invoked to explain both the reduced temperature gradient and its asymmetry. The interactive feedback between clouds and ice is probably the phenomenon that best explains the amplification of Arctic temperatures because as sea ice is removed there is a dramatic decrease in albedo and an increase in moisture source necessary for cloud formation.

The Arctic is clearly a bellwether for modern climate change. Arctic temperatures have increased more rapidly in response to anthropogenic greenhouse forcing than global temperatures (ACIA, 2004). Our independent proxy estimates indicate that Arctic temperatures during the Pliocene were considerably warmer than previous estimates derived from empirical proxies (Ballantyne et al., 2006; Elias and Matthews, 2002) and climate model simulations (Haywood et al., 2009), despite estimates of Pliocene atmospheric CO₂ levels that are comparable to today (Pagani et al., 2010). This indicates that climate models do not incorporate the full array of atmospheric, biospheric, and cryospheric feedback mechanisms necessary to simulate Arctic climate. Regardless of the feedback mechanism responsible for amplified Arctic temperatures, our results indicate that a significant increase in Arctic temperatures may be imminent in response to current atmospheric CO₂ levels.

ACKNOWLEDGMENTS

Ballantyne and Eberle were supported by NSF, Greenwood and Rybczynski were supported by the Natural Sciences and Engineering Research Council of Canada, and Sinnighe Damsté was supported by Netherlands Organization for Scientific Research and the European Research Council. This manuscript benefited from comments by C.R. Harington. This research was authorized by Nunavut's Department of Culture, Language, Elders and Youth, and

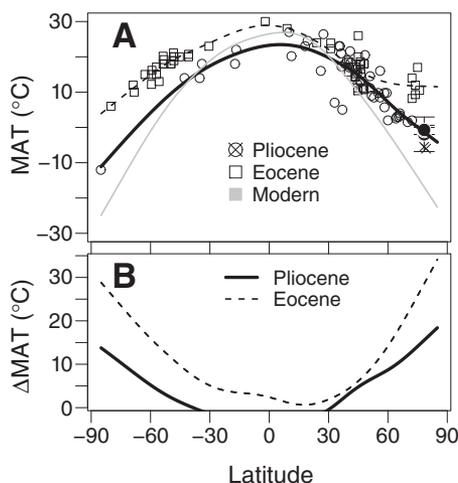


Figure 3. Pliocene temperature gradient in a global Cenozoic context. A: Gradients of mean annual temperature (MAT) are plotted for modern (gray line), Pliocene (black solid line), and early Eocene (black dashed line) by latitude. The three independent temperature estimates from this study are plotted as overlying filled black circles with standard error bars. Previous Pliocene MAT estimates from the Arctic (x) were not included when fitting the spline (see Table DR2 [see footnote 1]). B: Difference (Δ MAT) between modern MAT and Eocene (black dashed) and the Pliocene (black solid) are plotted for comparison.

the Qikiqtani Inuit Association. This is contribution 00310 to the Polar Continental Shelf Program and the International Polar Year.

APPENDIX

Site Description

The Beaver Pond site is an exceptionally well-preserved, organic-rich peat layer with many pieces of in situ wood (Ballantyne et al., 2006). The peat layer is embedded in a sandy deposit capped by a glacial deposit. A diverse assemblage of bryophytes, vascular plants, invertebrates, and vertebrates are represented by fossils found at this site (Fig. DR1 in the Data Repository). The mammalian taxa at this site correspond with taxa from North America and China that have been dated to be 4 to 5 m.y. old (Tedford and Harington, 2003).

Paleoclimate Proxies

Temperatures were first reconstructed using a novel approach based on branched glycerol dialkyl glycerol tetraethers present in the membranes of anaerobic soil bacteria abundant in peat bogs (Weijers et al., 2007). Tetraethers were extracted and analyzed as described by Weijers et al. (2007). The conservative total standard error associated with the MAT estimate based on this transfer function has been reported as 5.0 °C (Data Repository).

The second proxy we used to reconstruct Pliocene temperatures builds upon the multivariate approach of measuring oxygen isotopes ($\delta^{18}\text{O}$) and annual growth rings in fossil larch to estimate MAT (Ballantyne et al., 2006). We improved upon this approach by measuring $\delta^{18}\text{O}$ values in the cellulose of mosses to infer the $\delta^{18}\text{O}$ signature of the source water using a Finnigan MAT Delta Plus XL mass spectrometer (Data Repository).

The third temperature proxy was based on a comparison of plant taxa present at the site (Matthews and Ovenden, 1990) with nearest living relatives and their climatic ranges. Several databases of modern taxa were queried for nearest living relatives and their climatic ranges (see the Data Repository). We then used the coexistence approach of Mosbrugger and Utescher (1997), whereby a coexistence interval is calculated as the warmest minimum and coolest maximum MAT values for all nearest living relatives. We varied their method by expressing the MAT as the mean of the temperature range and expressing the error as the difference between MAT and the range of temperatures. The cold-month mean temperature (CMMT) and the warm-month mean temperature (WMMT) were calculated in the same manner.

Statistical Analysis

The distributions of MAT estimates derived for each proxy were evaluated using a two-tailed Student's *t*-test. To better approximate the distributions of MAT derived from the different proxies, we used a bootstrap technique (Efron and Tibshirani, 1997), whereby distributions were resampled with sample replacement 100,000 times and individual estimates were weighted by the inverse of their standard error (1/SE). Lastly, a composite distribution of Arctic Pliocene temperature estimates was derived by combining individual MAT estimates into a joint distribution and resampling according to the bootstrap technique. All statistical analyses were performed using R.

REFERENCES CITED

Abbot, D.S., and Tziperman, E., 2008, Sea ice, high-latitude convection, and equable climates: *Geophysical Research Letters*, v. 35, L03702, doi: 10.1029/2007GL032286.

ACIA, 2004, Impacts of a warming Arctic—Arctic climate impact assessment: Cambridge, UK, Cambridge University Press, 144 p.

Ballantyne, A.P., Ryzczynski, N., Baker, P.A., Harington, C.R., and White, D., 2006, Pliocene Arctic temperature constraints from the growth rings and isotopic composition of fossil larch: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 242, p. 188–200, doi: 10.1016/j.palaeo.2006.05.016.

Betts, A.K., and Ball, J.H., 1997, Albedo over the boreal forest: *Journal of Geophysical Research*, v. 102, p. 28,901–28,909, doi: 10.1029/96JD03876.

DeConto, R.M., Pollard, D., Wilson, P.A., Palike, H., Lear, C.H., and Pagani, M., 2008, Thresholds for Cenozoic bipolar glaciation: *Nature*, v. 455, p. 652–656, doi: 10.1038/nature07337.

Dowsett, H.J., 2007, The PRISM paleoclimate reconstruction and Pliocene sea-surface temperature, in Williams, M., et al., eds., Deep-time perspectives on climate change: Marrying the signal from computer models and biological proxies: *Micropaleontological Society Special Publication 2*, p. 459–480.

Dowsett, H.J., Cronin, T.M., Poore, R.Z., Thompson, R.S., Whatley, R.C., and Wood, A.M., 1992, Micropaleontological evidence for increased meridional heat transport in the North Atlantic Ocean during the Pliocene: *Science*, v. 258, p. 1133–1135, doi: 10.1126/science.258.5085.1133.

Efron, B., and Tibshirani, R.J., 1997, *An introduction to the bootstrap*: New York, Chapman and Hall, 450 p.

Elias, S.A., and Matthews, J.V., Jr., 2002, Arctic North American seasonal temperatures from the latest Miocene to the Early Pliocene, based on mutual climatic range analysis of fossil beetle assemblages: *Canadian Journal of Earth Sciences*, v. 39, p. 911–920, doi: 10.1139/e01-096.

Environment Canada, 2009, National Climate Data and Information Archive: Canadian Weather Office: www.climate.weatheroffice.ec.gc.ca.

Fedorov, A.V., Dekens, P.S., McCarthy, M., Ravelo, A.C., deMenocal, P.B., Barreiro, M., Pacanowski, R.C., and Philander, S.G., 2006, The Pliocene paradox (mechanisms for a permanent El Niño): *Science*, v. 312, p. 1485–1489, doi: 10.1126/science.1122666.

Greenwood, D.R., and Wing, S.L., 1995, Eocene continental climates and latitudinal temperature gradients: *Geology*, v. 23, p. 1044–1048, doi: 10.1130/0091-7613(1995)023<1044:ECCALT>2.3.CO;2.

Haywood, A.M., Chandler, M.A., Valdes, P.J., Salzmann, U., Lunt, D.J., and Dowsett, H.J., 2009, Comparison of mid-Pliocene climate predictions produced by the HadAM3 and GCMAM3 General Circulation Models: *Global and Planetary Change*, v. 66, p. 208–224, doi: 10.1016/j.gloplacha.2008.12.014.

Kump, L., and Pollard, D., 2008, Amplification of Cretaceous warmth by biological cloud feedbacks: *Science*, v. 320, p. 195, doi: 10.1126/science.1153883.

Lindsay, R.W., and Rothrock, D.A., 1994, Arctic sea ice albedo from AVHRR: *Journal of Climate*, v. 7, p. 1737–1749, doi: 10.1175/1520-0442(1994)007<1737:ASIAFA>2.0.CO;2.

Lunt, D.J., Foster, G.L., Haywood, A.M., and Stone, E.J., 2008, Late Pliocene Greenland glaciation controlled by a decline in atmospheric CO₂ levels: *Nature*, v. 454, p. 1102–1105, doi: 10.1038/nature07223.

Matthews, J.V., Jr., and Ovenden, L.E., 1990, Late Tertiary plant macrofossils from localities in

Arctic/Subarctic North America: A review of data: *Arctic*, v. 43, p. 364–392.

Morgan, K.R., and Bartholomew, G.A., 1982, Homeothermic response to reduced ambient temperature in a scarab beetle: *Science*, v. 216, p. 1409–1410, doi: 10.1126/science.216.4553.1409.

Mosbrugger, V., and Utescher, T., 1997, The coexistence approach—A method for quantitative reconstructions of Tertiary terrestrial palaeoclimate data using plant fossils: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 134, p. 61–86, doi: 10.1016/S0031-0182(96)00154-X.

Pagani, M., Liu, Z., LaRiviere, J., and Ravelo, A.C., 2010, High Earth-system climate sensitivity determined from Pliocene carbon dioxide concentrations: *Nature Geoscience*, v. 3, p. 27–30, doi: 10.1038/ngeo724.

Payne, R.E., 1972, Albedo of the sea surface: *Journal of the Atmospheric Sciences*, v. 29, p. 959–970, doi: 10.1175/1520-0469(1972)029<0959:AOTSS>2.0.CO;2.

Peterse, F., Kim, J.H., Schouten, S., Kristensen, D.K., Koç, N., and Sinninghe Damsté, J.S., 2009, Constraints on the application of the MBT/CBT palaeothermometer at high latitude environments (Svalbard, Norway): *Organic Geochemistry*, v. 40, p. 692–699, doi: 10.1016/j.orggeochem.2009.03.004.

Ravelo, A.C., Andreasen, D.H., Lyle, M., Lyle, O.L., and Wara, M.W., 2004, Regional climate shifts caused by gradual global cooling in the Pliocene epoch: *Nature*, v. 429, p. 263–267, doi: 10.1038/nature02567.

Robinson, M.M., 2009, New quantitative evidence of extreme warmth in the Pliocene Arctic: *Stratigraphy*, v. 6, p. 265–275.

Stickley, C.E., St. John, K., Koc, N., Jordan, R.W., Passchier, S., Pearce, R.B., and Kearns, L.E., 2009, Evidence for middle Eocene Arctic sea ice from diatoms and ice-rafted debris: *Nature*, v. 460, p. 376–379, doi: 10.1038/nature08163.

St. John, K.E.K., and Krissek, L.A., 2002, The late Miocene to Pleistocene ice-rafting history of southeast Greenland: *Boreas*, v. 31, p. 28–35, doi: 10.1080/03009480210651.

Strathdee, A.T., and Bale, J.S., 1998, Life on the edge: Insect ecology in Arctic environments: *Annual Review of Entomology*, v. 43, p. 85–106.

Sugimoto, A., Yanagisawa, N., Naito, D., Fujita, N., and Maximov, T.C., 2002, Importance of permafrost as a source of water for plants in east Siberian taiga: *Ecological Research*, v. 17, p. 493–503, doi: 10.1046/j.1440-1703.2002.00506.x.

Tedford, R.H., and Harington, C.R., 2003, An Arctic mammal fauna from the Early Pliocene of North America: *Nature*, v. 425, p. 388–390, doi: 10.1038/nature01892.

Weijers, J.W.H., Schouten, S., van den Donker, J.C., Hopmans, E.C., and Sinninghe Damsté, J.S., 2007, Environmental controls on bacterial tetraether membrane lipid distribution in soils: *Geochimica et Cosmochimica Acta*, v. 71, p. 703–713, doi: 10.1016/j.gca.2006.10.003.

Zachos, J.C., Dickens, G.R., and Zeebe, R.E., 2008, An early Cenozoic perspective on greenhouse warming and carbon-cycle dynamics: *Nature*, v. 451, p. 279–283, doi: 10.1038/nature06588.

Manuscript received 27 October 2009

Revised manuscript received 29 January 2010

Manuscript accepted 2 February 2010

Printed in USA