Science
AAAS

Northern Hemisphere Controls on Tropical Southeast African Climate During the Past 60,000 Years

Jessica E. Tierney, *et al.*

Science **322**, 252 (2008);
DOI: 10.1126/science.1160485

6. S. R. McNutt, in *Monitoring and Mitigation of Volcanic Hazards*, R. Scarpa, R. Tilling, Eds. (Springer Verlag, Berlin, 1996), pp. 99–146.
7. R. Scandone, K. V. Cashman, S. D. Malone, *Earth Planet. Sci. Lett.* **253**, 513 (2007).
8. J. W. Neuberg *et al.*, *Geotherm. Res.* **153**, 37 (2006).
9. G. Rogers, H. Dragert, *Science* **300**, 1942 (2003).
10. Y. Ito *et al.*, *Science* **315**, 503 (2007).
11. P. M. Benson *et al.*, *Geophys. Res. Lett.* **34**, 10.1029/2006GL028721 (2007).
12. AE has its origin in mechanical engineering and high-pressure hydraulics, where it is frequently used to detect leaks from gas tanks (such as liquified petroleum gas flashing to gas). The turbulent flow generates AE.
13. K. Aki, P. Richards, *Quantitative Seismology* (University Science Books, Sausalito, CA, ed. 2, 2002).
14. D. Patane *et al.*, *Science* **299**, 2061 (2003).
15. P. M. Benson, S. Vinciguerra, P. G. Meredith, R. P. Young, paper presented at the 29th Course of the International School of Geophysics Euro-Conference of Rock Physics and Geomechanics, Erice, Sicily, 28 September, 2007.
16. D. C. Collins, W. S. Pettitt, R. P. Young, *Pure Appl. Geophys.* **159**, 197 (2002).
17. S. Stanchits *et al.*, *Pure Appl. Geophys.* **163**, 975 (2006).
18. S. Miller *et al.*, *Nature* **427**, 10.1038/nature02251 (2004).
19. D. A. Lockner *et al.*, *Nature* **350**, 39 (1991).
20. G. R. Foulger *et al.*, *Geotherm. Res.* **132**, 45 (2004).
21. H. Kumagai, B. A. Chouet, M. Nakano, *J. Geophys. Res.* **107**, 10.1029/2001JB001704 (2002).
22. M. R. James *et al.*, *Geotherm. Res.* **129**, 61 (2004).
23. M. R. James *et al.*, *J. Geophys. Res.* **111**, 10.1029/2005JB003718 (2006).
24. B. R. Julian, *J. Geophys. Res.* **99**, 10.1029/93JB03129 (1994).
25. H. Tuffen, D. Dingwell, *Bull. Volcanol.* **67**, 370 (2005).
26. L. Burlini *et al.*, *Geology* **35**, 183 (2007).
27. I. G. Main, *Nature* **357**, 27 (1992).
28. C. G. Hatton, I. G. Main, P. G. Meredith, *Nature* **367**, 160 (1994).
29. C. A. Rowe *et al.*, *Geophys. Res. Lett.* **25**, 2297 (1998).
30. This work was supported by a Marie-Curie International Fellowship within the 6th European Community Framework program (contract MOIF-CT-2005-020167 to P.M.B.), project FIRB-MIUR (Sviluppo Nuove Tecnologie per la Protezione e Difesa del Territorio dai Rischi Naturali) to S.V.; and a Canadian Foundation for Innovation award to R.P.Y. The authors thank L. Malagnini and J. Neuberg for fruitful discussions, A. Cavallo for FESEM technical support at the HT-HP laboratory (INGV Rome), and two anonymous reviewers for comments that greatly helped to improve this manuscript.

Supporting Online Material
www.sciencemag.org/cgi/content/full/322/5899/249/DC1
Figs. S1 to S3
Reference

17 June 2008; accepted 4 September 2008
10.1126/science.1161927

Northern Hemisphere Controls on Tropical Southeast African Climate During the Past 60,000 Years

Jessica E. Tierney,[1]* James M. Russell,[1] Yongsong Huang,[1]
Jaap S. Sinninghe Damsté,[2] Ellen C. Hopmans,[2] Andrew S. Cohen[3]

The processes that control climate in the tropics are poorly understood. We applied compound-specific hydrogen isotopes (δD) and the TEX_{86} (tetraether index of 86 carbon atoms) temperature proxy to sediment cores from Lake Tanganyika to independently reconstruct precipitation and temperature variations during the past 60,000 years. Tanganyika temperatures follow Northern Hemisphere insolation and indicate that warming in tropical southeast Africa during the last glacial termination began to increase ~3000 years before atmospheric carbon dioxide concentrations. δD data show that this region experienced abrupt changes in hydrology coeval with orbital and millennial-scale events recorded in Northern Hemisphere monsoonal climate records. This implies that precipitation in tropical southeast Africa is more strongly controlled by changes in Indian Ocean sea surface temperatures and the winter Indian monsoon than by migration of the Intertropical Convergence Zone.

The mechanisms that cause fluctuations of rainfall and temperature in the tropics—home to a large portion of the world's population and a region of central importance to the global hydrologic cycle—are poorly understood. One process often invoked to explain past changes in tropical precipitation and temperature is a shift in the mean annual position of the Intertropical Convergence Zone (ITCZ), which migrates meridionally in response to seasonally and orbitally driven changes in interhemispheric heat distribution (*1*, *2*). However, loci of tropical precipitation and convergence within the ITCZ itself respond to changes in sea surface temperatures (SSTs) and coupled ocean-atmosphere zonal modes, such as El Niño–Southern Oscillation and the Indian Ocean Dipole (IOD) (*3*, *4*), as well as the strength of the monsoons that bring moisture into the continents (*5*). The importance of these zonal forces acting on tropical rainfall, vis-à-vis changes in ITCZ position, is incompletely understood, in part because long, high-resolution paleoclimatic reconstructions that constrain tropical rainfall and temperature are rare.

[1]Department of Geological Sciences, Brown University, Providence, RI 02912, USA. [2]Department of Marine Organic Biogeochemistry, Royal Netherlands Institute for Sea Research (NIOZ), 1790 AB Den Burg, Netherlands. [3]Department of Geosciences, University of Arizona, Tucson, AZ 85721, USA.

*To whom correspondence should be addressed. E-mail: Jessica_Tierney@brown.edu

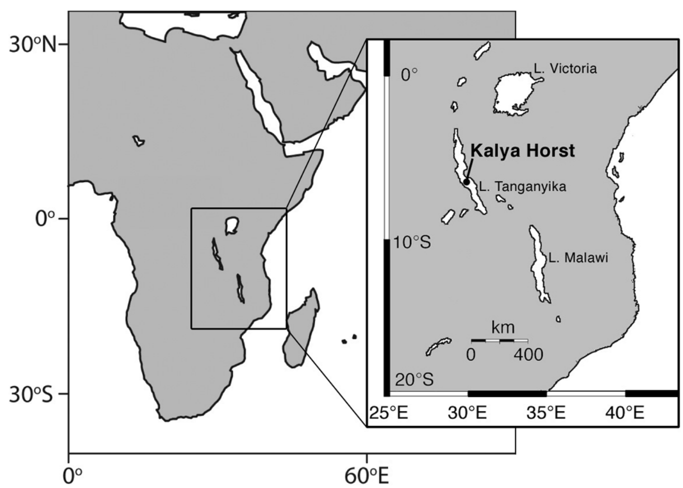

Fig. 1. Map of East Africa and Lake Tanganyika. Two Kullenberg piston cores collected from the Kalya Horst (S 6°42′, E 29°50′) in 2004 (cores NP04-KH04-3A-1K and NP04-KH04-4A-1K) were selected to compile a continuous sedimentary record for the past 60,000 years. The Tanganyika basin and watershed span 2° to 10°S, covering much of the southeast African tropics. See SOM text 1 for regional climatology.

Tropical Africa is a site of deep tropical convection and contains a population that is economically vulnerable to climatic change. The African Great Lakes, situated in the East African Rift Valley, are excellent archives of climate change in tropical East Africa. Reconstructions of lake level fluctuations establish that East Africa was generally dry during the Last Glacial Maximum (LGM), humid during the early Holocene, and dry during the late Holocene (*6*). Furthermore, high-resolution records from these lakes based on indicators such as fossil pollen, geochemistry, and lithology show that East African environmental changes are linked to global climate processes on millennial time scales (*7*–*11*). Yet available records from East Africa rarely extend beyond the LGM and do not independently constrain rainfall and temperature. This has confounded the interpretation of humid and arid intervals in this region; the Younger Dryas, for example, is variously thought to be wet and dry in tropical southeast Africa (*8*, *11*).

To better understand the controls on East African temperature and hydrology, we applied the TEX_{86} (tetraether index of 86 carbon atoms) paleotemperature proxy together with hydrogen isotopic analyses of terrestrial leaf waxes to sediment cores from Lake Tanganyika, at an average time step of 300 years (Fig. 1). TEX_{86} is based on the relative degree of cyclization of aquatic archaeal glycerol dialkyl glycerol tetraether (GDGT) isoprenoidal lipids; is linearly correlated with temperature (*12*); and can be applied to reconstruct the temperature of some large lakes, including Lake Tanganyika (*13*, *14*) [supporting online material (SOM) text 2].

Terrestrial plants are the dominant source of long-chain (C_{26} to C_{30}) monocarboxylic fatty acids in lacustrine sediments, and their deuterium/hydrogen (D/H) ratio is an excellent indicator of terrestrial hydrologic conditions (*15*, *16*). We analyzed the δD of the C_{28} *n*-acid [hereafter $\delta D_{leaf\ wax}$, expressed in per mil versus Vienna standard mean ocean water (SMOW) values], the most abundant fatty acid in our cores. Because the isotopic fractionation that occurs during leaf wax synthesis appears consistent across different plant types (due to the interactive effects of vegetation type and relative humidity), $\delta D_{leaf\ wax}$ reflects changes in the δD of precipitation (*15*). The primary control on δD of tropical East African precipitation is the "amount effect" (*17*), although moisture source and history may play a secondary role. Thus, higher δD values indicate reduced precipitation, and lower values represent wet periods.

Our TEX_{86} and $\delta D_{leaf\ wax}$ reconstructions show that temperature and hydrology in the Tanganyika basin were extremely variable throughout the past 60,000 years (Fig. 2). Holocene lake surface temperature (LST) fluctuated between ~27° and 29°C, whereas temperatures during the LGM were ~4°C cooler. The magnitude and timing of this temperature shift are similar to those of nearby Lake Malawi (*14*), indicating that our TEX_{86} record captures regional temperature change in tropical southeast Africa during deglaciation.

$\delta D_{leaf\ wax}$ spans a range of ~50 per mil (‰,) and records numerous abrupt shifts between arid and humid conditions throughout the past 60,000 years. During marine isotope stage (MIS) 3, rapid excursions toward enriched $\delta D_{leaf\ wax}$ values indicate millennial-scale pulses of aridity, the most pronounced of which is centered at 37,255 years before the present (yr B.P.) ± 917 yr B.P. This event is coincident with Heinrich event 4 (H4), which occurred at 38,000 yr B.P. and is the largest of the six Heinrich events during MIS 3 in the North Atlantic (*18*). It is possible that arid events at 47,500 and 57,000 yr B.P. in our record are associated with H5 and H6 (Fig. 3), although our age control is not sufficient to constrain their timing. A positive 15‰ shift in $\delta D_{leaf\ wax}$ at ~16,700 yr B.P. indicates that the most arid conditions of the past 60,000 years occurred during H1, yet we do not observe changes in $\delta D_{leaf\ wax}$ during H2 and H3. The dramatic expression of H4 and H1 in our record and the lack of H2 and H3 suggest a variable sensitivity of climate in the Tanganyika basin to North Atlantic climate processes, possibly due to the different magnitudes of the Heinrich events themselves and their ability to propagate into the southern tropics.

Climate in the Tanganyika basin switched from arid conditions during the LGM and H1 to humid conditions in the early Holocene in two rapid steps. A 260-year-long 17‰ decrease in $\delta D_{leaf\ wax}$ occurs at 15,100 yr B.P., coincident with the onset of the Bølling period (*19*), followed by a 270-year-long 23‰ decrease at 11,600 yr B.P., the end of the Younger Dryas (*19*) (Fig. 3). The early Holocene was the wettest period in our record, as indicated by $\delta D_{leaf\ wax}$ values that are depleted by 30‰ relative to late Holocene values. The transition toward a more arid late Holocene at about 4,700 yr B.P. was also abrupt, occurring within 300 years. Such rapid changes from humid to arid conditions are a persistent feature of our $\delta D_{leaf\ wax}$ record, suggesting that rainfall in this region responds in a nonlinear fashion to changing climatic parameters.

Tanganyika LST did not cool during the millennial-scale arid intervals recorded by $\delta D_{leaf\ wax}$ (Fig. 3). However, precipitation and temperature do co-vary on orbital time scales (Fig. 2). Shifts between warm/wet and cool/dry conditions follow Northern Hemisphere summer insolation, as opposed to austral summer or annual insolation at 6°S, indicating that the heat and moisture budget of this part of Africa is dynamically linked to the Northern Hemisphere.

In particular, Tanganyika LST at the end of the LGM follows rising Northern Hemisphere summer insolation, a potential trigger for deglaciation (*20*). Temperatures rise at 20,000 ± 380 yr B.P., just as they do in a TEX_{86} LST record from Lake Malawi (*14*) (Fig. 3). This timing is consistent with rising temperatures at ~20,000 yr B.P. in Antarctica, yet leads the deglacial CO_2 rise recorded in Antarctic ice cores (*21*) by about 3,000 years, a difference that is outside the chronological errors of the ice core and the LST records. Increasing greenhouse gas concentrations are therefore not responsible for the initial transmission of warming from the high latitudes to the southeast African tropics. Yet a rapid, presumably atmospheric, communication mechanism must exist for this region to "feel" Northern Hemisphere insolation. Aside from CO_2, changes in the hydrologic cycle are suspect, but our $\delta D_{leaf\ wax}$ record indicates that precipitation did not increase until 15,100 yr B.P. Thus, the mechanism linking deglacial temperature changes between high and low latitudes remains elusive.

Our $\delta D_{leaf\ wax}$ data are remarkably similar to isotopic records of the Asian monsoon from Hulu and Dongge Caves in China (*22*, *23*), with arid events occurring during the Younger Dryas, H1, and H4 to H6; a wet early Holocene; and a dry late Holocene, although the timing of their respective transitions to a more arid late Holocene is different (Fig. 3). This in-phase behavior is surprising, because Northern and Southern Hemisphere rainfall records should be out of phase if ITCZ position were the dominant control on rainfall variability in the Tanganyika basin. During the early Holocene "African Humid Period," for example, the ITCZ was situated farther north over Africa (*24*), and the region around Lake Tanganyika should have become more arid as the ITCZ spent less time in the southern tropics. Likewise, we observe that the Younger Dryas was arid in the Tanganyika basin, though a southward shift of the ITCZ would predict humid conditions (*2*, *9*). Proxy evidence from Lake Malawi also indicates

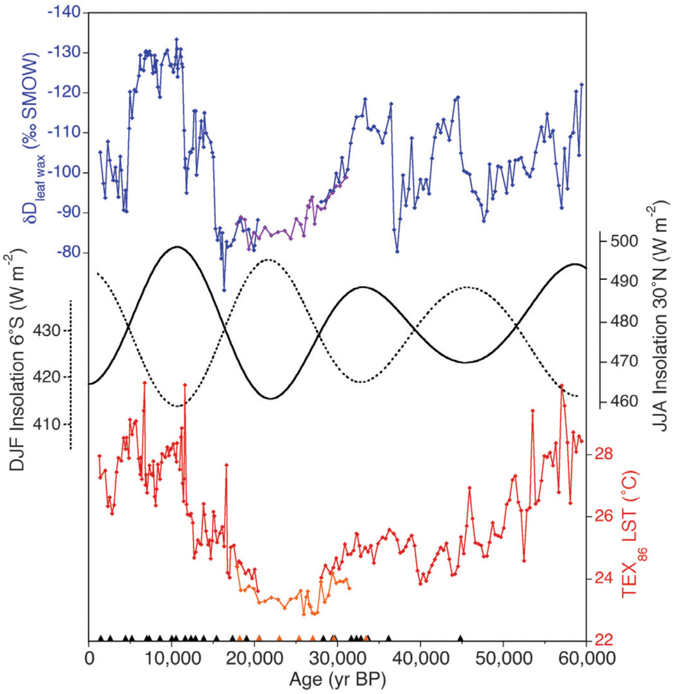

Fig. 2. $\delta D_{leaf\ wax}$ and TEX_{86} LST from Lake Tanganyika. $\delta D_{leaf\ wax}$ and TEX_{86} data from core NP04-KH04-3A-1K are plotted in blue and red, and data from core NP04-KH04-4A-1K are plotted in purple and orange. The TEX_{86} data show a 0.5° offset between the two cores; this is probably due to core NP04-KH04-4A-1K's more proximal location to the eastern shore of the lake, where seasonal coastal upwelling occurs today (SOM text 3). $\delta D_{leaf\ wax}$ data line up well between cores, reflecting the regional character of the proxy. Chronology is constrained by 33 ^{14}C AMS dates, which are plotted for NP04-KH04-3A-1K and NP04-KH04-4A-1K as black and orange triangles, respectively (SOM materials and methods). June-July-August (JJA) insolation for 30°N (solid line) emphasizes the Northern Hemisphere influence evident in the temperature and precipitation data. December-January-February (DJF) insolation for the local area (6°S) (dotted line) is shown for contrast.

that the Younger Dryas and H1 to H5 were dry (*10*, *11*), implying that precipitation patterns over much of tropical southeast Africa did not respond predictably to ITCZ migration. This behavior is distinctly different from the rainfall history of southern tropical South America, which is clearly anti-phased with the Northern Hemisphere (*25*).

If ITCZ position alone cannot explain rainfall variability in tropical southeast Africa, factors controlling the advection of moisture to the ITCZ, as well as the strength of convergence itself, must be implicated. Indeed, SSTs, which control latent heat flux into the atmosphere; ocean-basin SST gradients, which influence large-scale atmospheric circulation patterns; and the strength of the winds that advect humidity into the continents are all important to tropical African precipitation (*26*, *27*). These factors could effect changes in precipitation in the Lake Tanganyika basin via several different mechanisms. Wet conditions could arise from an increase in Atlantic Ocean moisture flux via the Congo basin, as proposed by Schefuß *et al*. (*27*) to explain humid conditions during the early Holocene in central Africa. However, moisture flux into the Congo basin is low at ~11,000 yr B.P. and does not reach a maximum until ~8,000 yr B.P. (*27*), which is substantially different from the timing of changes in $\delta D_{leaf\ wax}$ that we observe in Lake Tanganyika.

Alternatively, we argue that changes in moisture flux into Africa from the Indian Ocean basin control East African precipitation variability. Modern precipitation in southeast Africa is highly seasonal, occurring from October to April, and most of this moisture is derived from the Indian Ocean (*28*). Thus, we expect precipitation to vary in concert with Indian Ocean SSTs (which govern the generation of moisture), as well as the strength of the winter Indian monsoon circulation (which affects the transport of moisture). Although the winter and summer monsoons are commonly thought to work in opposition to one another (*29*), global climate modeling experiments show that on orbital time scales, increases in Northern Hemisphere precession result in amplified seasonality that should intensify both the summer and winter monsoons (*30*, *31*). A more vigorous winter Indian monsoon, then, could explain the humid conditions that prevailed in the Tanganyika basin during the Early Holocene as well as during precession maxima in MIS 3.

Winter monsoon strength does not, however, satisfactorily explain the arid episodes we observe during the Younger Dryas, H1, and H4. Zr/Ti data from Lake Malawi indicate strong northerly winds in southeast Africa during these events (*10*), implying vigorous winter monsoon circulation and a southward migration of the ITCZ. Yet these events are distinctly arid in both the Tanganyika and Malawi basins. We therefore surmise that cold SSTs during millennial-scale stadials reduced latent heat flux from the western Indian Ocean, minimizing the amount of moisture transported into East Africa by the winter monsoon. Data from the Pakistan margin that indicate cooler SSTs during millennial-scale stadials in MIS 3 support this hypothesis (*32*).

Thus the mechanisms controlling precipitation in tropical southeast Africa evidently vary over different time scales, though they are not necessarily mutually exclusive; Indian Ocean SSTs may also play a role in influencing orbital-scale changes in East African rainfall. During the early Holocene, enhanced cooling in the eastern Indian Ocean is thought to have modified Walker circulation over the basin, producing longer and more frequent positive IOD events (*30*). The positive IOD phase is associated with warmer SSTs in the western Indian Ocean, an intensification of convergence, and an increase in East African rainfall (*4*). This mechanism, along with an increase in the Indian seasonal monsoons, could account for the humid conditions that characterize tropical East Africa during this time.

The fact that both temperature and precipitation in the Tanganyika basin show many characteristics of Northern Hemisphere climatic variability demonstrates that the Northern Hemisphere has a substantial influence on climate in tropical southeast Africa. An early warming during the last deglaciation highlights the importance of atmospheric teleconnections linking the high and low latitudes, although the mechanisms behind this relationship remain unknown. Although ITCZ migration strongly influences East African climate by modifying seasonal wind strength (*9*, *10*), it is apparently not the dominant control on precipitation variability in tropical southeast Africa; rather, oceanic and atmospheric factors controlling moisture generation and advection heavily influence rainfall variability in this region. Particularly, the highly nonlinear character of our $\delta D_{leaf\ wax}$ record implies that precipitation regimes in East Africa are liable to change abruptly in response to climatic forcing. This behavior has implications for modeling the response of East African hydrology to anthropogenic climate change.

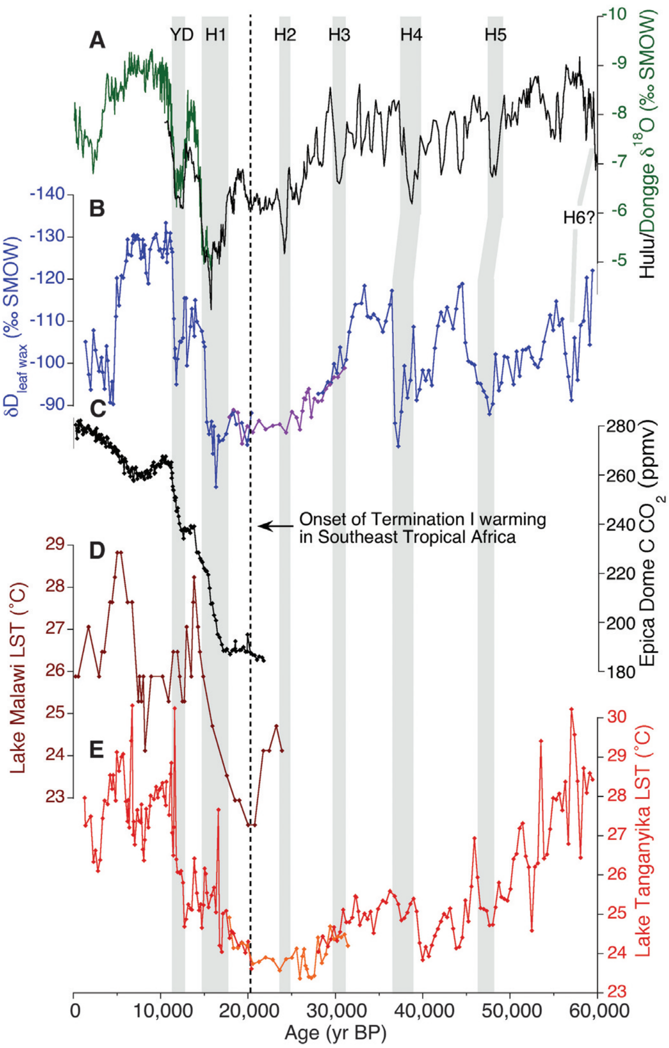

Fig. 3. Comparison of Lake Tanganyika TEX_{86} and $\delta D_{leaf\ wax}$ data with other records of paleoclimate. Records are plotted as follows: (**A**) $\delta^{18}O$ data from Hulu and Dongge caves (*22*, *23*). (**B**) Lake Tanganyika $\delta D_{leaf\ wax}$. (**C**) Deglacial CO_2 record from the Epica Dome C ice core (*21*). (**D**) Lake Malawi TEX_{86} LST (*14*). (**E**) Lake Tanganyika TEX_{86} LST, with the NP04-KH04-4A-1K values corrected for the 0.5°C offset described in Fig. 2. Gray bars indicate the Younger Dryas (YD) and H1 to H6 as recorded in Hulu Cave and Lake Tanganyika. The onset of warming in East Africa is marked with a dotted vertical line.

References and Notes

1. G. H. Haug, K. A. Hughen, D. M. Sigman, L. C. Peterson, U. Röhl, *Science* **293**, 1304 (2001).
2. D. W. Lea, D. K. Pak, L. C. Peterson, K. A. Hughen, *Science* **301**, 1361 (2003).
3. C. M. Moy, G. O. Seltzer, D. T. Rodbell, D. M. Anderson, *Nature* **420**, 162 (2002).
4. N. H. Saji, B. N. Goswami, P. N. Vinayachandran, T. Yamagata, *Nature* **401**, 360 (1999).
5. P. J. Webster *et al*., *J. Geophys. Res.* **103**, 14451 (1998).
6. F. Gasse, *Quat. Sci. Rev.* **19**, 189 (2000).
7. R. Bonnefille, F. Chalié, *Global Planet. Change* **26**, 25 (2000).

8. Y. Garcin, A. Vincens, D. Williamson, J. Guiot, G. Buchet, *Geophys. Res. Lett.* **33**, 10.1029/2005GL025531 (2006).
9. J. E. Tierney, J. M. Russell, *Geophys. Res. Lett.* **34**, 10.1029/2007GL029508 (2007).
10. E. T. Brown, T. C. Johnson, C. A. Scholz, A. S. Cohen, J. W. King, *Geophys. Res. Lett.* **34**, 10.1029/2007GL031240 (2007).
11. I. S. Castañeda, J. P. Werne, T. C. Johnson, *Geology* **35**, 823 (2007).
12. J. Kim, S. Schouten, E. C. Hopmans, B. Donner, J. S. Sinninghe Damsté, *Geochim. Cosmochim. Acta* **72**, 1154 (2008).
13. L. A. Powers *et al.*, *Geology* **32**, 613 (2004).
14. L. A. Powers *et al.*, *Geophys. Res. Lett.* **32**, 10.1029/2004GL022014 (2005).
15. J. Hou, W. D'Andrea, Y. Huang, *Geochim. Cosmochim. Acta* **72**, 3503 (2008).
16. B. Shuman, Y. Huang, P. Newby, Y. Wang, *Quat. Sci. Rev.* **25**, 2992 (2006).
17. M. Vuille, M. Werner, R. S. Bradley, F. Keimig, *J. Geophys. Res.* **110**, 10.1029/2005JD006022 (2005).
18. S. R. Hemming, *Rev. Geophys.* **42**, 1 (2004).
19. R. B. Alley, P. U. Clark, *Annu. Rev. Earth Planet. Sci.* **27**, 149 (1999).
20. K. Kawamura *et al.*, *Nature* **448**, 912 (2007).
21. E. Monnin *et al.*, *Science* **291**, 112 (2001).
22. Y. J. Wang *et al.*, *Science* **294**, 2345 (2001).
23. D. Yuan *et al.*, *Science* **304**, 575 (2004).
24. P. deMenocal *et al.*, *Quat. Sci. Rev.* **19**, 347 (2000).
25. X. Wang *et al.*, *Geophys. Res. Lett.* **34**, 10.1029/2007GL031149 (2007).
26. P. Barker, F. Gasse, *Quat. Sci. Rev.* **22**, 823 (2003).
27. E. Schefuß, S. Schouten, R. R. Schneider, *Nature* **437**, 1003 (2005).
28. Y. Zhu, R. E. Newell, *Mon. Weather Rev.* **126**, 725 (1998).
29. G. Yancheva *et al.*, *Nature* **445**, 74 (2007).
30. N. J. Abram *et al.*, *Nature* **445**, 299 (2007).
31. A. B. G. Bush, *Global Planet. Change* **32**, 331 (2002).
32. M. J. Higginson, M. A. Altabet, L. Wincze, T. D. Herbert, D. W. Murray, *Paleoceanography* **19**, 10.1029/2004PA001031 (2004).

33. We thank two anonymous reviewers for their insightful comments; S. Schouten, S. Clemens, and T. Herbert for their suggestions on earlier drafts of the manuscript; and M. Alexandre, N. Meyer, J. Ossebaar, and I. Castañeda for analytical assistance. This research was supported by NSF-EAR 0639474 to J.R., the Nyanza Project (grants NSF-ATM 0223920 and BIO 0383765, to A.C.), and the National Defense Science and Engineering Graduate Fellowship to J.T. The authors declare that they have no competing financial interests.

Supporting Online Material
www.sciencemag.org/cgi/content/full/1160485/DC1
Materials and Methods
SOM Text
Figs. S1 to S6
Tables S1 to S3
References

14 May 2008; accepted 2 September 2008
Published online 11 September 2008;
10.1126/science.1160485
Include this information when citing this paper.

Natural Selection on a Major Armor Gene in Threespine Stickleback

Rowan D. H. Barrett,* Sean M. Rogers, Dolph Schluter

Experimental estimates of the effects of selection on genes determining adaptive traits add to our understanding of the mechanisms of evolution. We measured selection on genotypes of the *Ectodysplasin* locus, which underlie differences in lateral plates in threespine stickleback fish. A derived allele (low) causing reduced plate number has been fixed repeatedly after marine stickleback colonized freshwater from the sea, where the ancestral allele (complete) predominates. We transplanted marine sticklebacks carrying both alleles to freshwater ponds and tracked genotype frequencies over a generation. The low allele increased in frequency once lateral plates developed, most likely via a growth advantage. Opposing selection at the larval stage and changing dominance for fitness throughout life suggest either that the gene affects additional traits undergoing selection or that linked loci also are affecting fitness.

Adaptive evolution occurs when genetic variation affects phenotypes under selection. This process has been detected by the discovery of candidate genes underlying phenotypic traits whose adaptive significance is known or suspected (*1*–*7*) and by identifying statistical signatures of selection on genomic regions affecting phenotypic traits (*8*–*12*). However, field experiments evaluating the fitness consequences of allelic substitutions at candidate loci should provide estimates of the timing and strength of selection, enhance understanding of the genetics of adaptation, and yield insights into the mechanisms driving changes in gene frequency.

Freshwater threespine sticklebacks (*Gasterosteus aculeatus*) originated from marine populations that invaded newly created coastal lakes and streams throughout the Northern Hemisphere following the last ice age. Within the past 20,000 years or less, freshwater populations repeatedly underwent a loss in bony armor plating (*13*). Marine sticklebacks are typically armored with a continuous row of 30 to 36 bony lateral plates on each side (complete morph), whereas freshwater sticklebacks typically have 0 to 9 plates (low morph) or, less often, an intermediate number of plates (partial morph) (*13*–*15*) (Fig. 1). Armor reduction following colonization of freshwater evolved rapidly (*16*–*19*) from the fixation of a clade of low alleles of the *Ectodysplasin* gene (hereafter, the *Eda* low allele). This allele evolved ~2 million years ago and is rare (~1%) in the ocean (*1*). The repeated fixation of this allele implies that it undergoes positive selection in freshwater, because genetic drift alone is unlikely to produce a strong correlation between phenotype and environment (*20*–*22*).

Fish with reduced armor have a juvenile growth advantage (*23*), which may result from the higher cost of mineralizing bone in freshwater (*24*, *25*), which has low ion concentrations relative to marine environments. This increased growth rate should, in turn, reduce predation by insects (*26*), as well as increase lipid stores, which results in higher over-winter survival (*27*). Larger fish also may breed earlier (*28*) and have access to better terri-

Fig. 1. Lateral plate morphs in marine stickleback. Complete morph (top), partial morph (middle), and low morph (bottom). Fish were stained with Alizarin red to highlight bone.

Zoology Department and Biodiversity Research Centre, University of British Columbia, 6270 University Boulevard, Vancouver, BC V6T 1Z4, Canada.

*To whom correspondence should be addressed. E-mail: rbarrett@zoology.ubc.ca