

After a decay of 4 days, 5 days, 7 days, and 8 days, samples were remeasured on a high-resolution Ge detector system (resolution of 1.61 KeV for the Co^{60} , 1332 KeV photopeak). The same sample material used above was then fused with a combination of lithium metaborate/tetraborate and lithium carbonate in high-purity graphite crucibles covered with graphite lids in an induction furnace. The molten mixture was transferred to a 5% (by volume) nitric acid (with Cd internal standard) solution. The molten bead immediately shattered and was shaken until totally dissolved (~15 min). Masses of 0.05-g aliquots in duplicate were analyzed by combustion-IR techniques using an ELTRA simultaneous carbon/sulfur analyzer, Model 800. A sequence of 0.1-g aliquots were digested with aqua regia at 90°C for 2 hours. Finally, a 0.1-g aliquot was subjected to an 18-hour ramped digestion in Teflon test tubes using hydrochloric, nitric, perchloric, and hydrofluoric acids. Samples were analyzed by ICP-optical emission spectrometry (OES) on a Perkin-Elmer OPTIMA 3000 ICP-OES and a Perkin-Elmer SCIEX ELAN 6000 and 6100. We noted systematically higher values in all cases for degraded (immersed in lake water) as compared to pristine meteorite abundances, except for H, Na, and Cl, which were much lower in the degraded specimens than in the pristine material. The H anom-

aly is probably due to excess removal of indigenous water in the degraded sample; it is very common for Cl chondrites to contain large amounts (in excess of 10 wt %) of primordial water [L. Baker *et al.*, *Lunar Planet. Sci.* **XXIX**, 1740 (1998)]. The large difference in Na and Cl between pristine and water-soaked samples might be interpreted as removal of water-soluble halite from Tagish Lake. Halite has been previously reported in H chondrites [M. E. Zolensky *et al.*, *Science* **285**, 1377 (1999)]. This indirect indication of halite in a carbonaceous chondrite would therefore be unsurprising.

23. H. Y. McSween, *Rev. Geophys. Space Phys.* **17**, 1059 (1979).
24. K. Tomeoka, H. Kojima, K. Yanai, *Proc. NIPR Symp. Antarct. Meteorites* **2**, 36 (1989).
25. E. L. Hoffman *et al.*, *Anal. Chem. Acta* **102**, 157 (1978).
26. K. Lodders and B. Fegley, *The Planetary Scientist's Companion* (Oxford Univ. Press, Oxford, 1998), pp. 314–316.
27. We thank J. Brook, D. Stangel, and M. Brook for assistance in meteorite recovery work; R. Halliday, M. Jasek, E. Magnuson, and C. R. Roots for assistance in interviewing and locating the many eyewitnesses in the Yukon and British Columbia, who also provided still photos and video of the fireball dust cloud; the

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The Last Glacial–Holocene Transition in Southern Chile

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Warming at the last glacial termination in the North Atlantic region was interrupted by a period of renewed glacial activity during the Younger Dryas chronozone (YDC). The underlying mechanism of this cooling remains elusive, but hypotheses turn on whether it was a global or a North Atlantic phenomenon. Chronological, sedimentological, and palaeoecological records from sediments of small lakes in oceanic southern Chile demonstrate that there was no YDC cooling in southern Chile. It is therefore likely that there was little or no cooling in southern Pacific surface waters and hence that YDC cooling in the North Atlantic was a regional, rather than global, phenomenon.

The YDC [13 to 11.2 thousand years before the present (ky BP) (1)] in northern Europe was a period of renewed glacial activity after the decline of the main last glacial ice mass. The temperature changes of the period are seen most strongly in oceanic western Europe, and their amplitude decreases eastward into the continental interior (2). A cooling during this period has also been recognized in eastern North America (3) and correlated with event stratigraphy from the Greenland Ice Core Project (GRIP) (4). Here we present chronological, sedimentological, and pollen data from the sediments of small lakes in oceanic southern Chile (44° to 47°S), chosen to be as similar as possible in character and location to sites in the North Atlantic region

that demonstrate strong temperature changes during the YDC. We show that there was no cooling and that the YDC was a period of continuing forest development and increasing diversity. The climate of this region is dominated by air masses from the Pacific and the north-flowing Humboldt Current, which originates as an eastward flow across the southern Pacific (5). If there was no cooling during the YDC in southern Chile, it is unlikely that there can have been any cooling in southern Pacific surface waters; hence, the cooling during the YDC in the North Atlantic was a regional, rather than global, phenomenon.

In temperate areas of moderate and high precipitation, small lakes remain full to their outlets, retaining a constant deep-water anoxic environment at their base. The sediments in such lakes consist largely of the remains of planktonic algae, atmospheric dust, and material washed from surrounding slopes. Such sediments may thus be highly stable as sedimentary environments, preserving materials indicative of conditions in aquatic, terrestrial, and atmospheric environments. We sampled

the sediments of a series of lakes on the Taitao peninsula and an islands of the Chonos archipelago in southern Chile (Fig. 1), choosing lakes that were located in rock basins, had no inflowing streams, and were still moderately deep (2 to 5 m) for their size (100 m diameter). Such sites should be the most sensitive to any temperature changes of the period, as in western Europe (6–8). Cores were collected with a Livingstone piston corer. On return to the laboratory, they were analyzed immediately for physical properties and sampled for radiocarbon dating [bulk and accelerator mass spectrometry (AMS)] and the presence of tephtras to provide a chronology, and the pollen content was assessed at intervals of 100 to 150 years or less.

All cores from these lakes showed similar simple stratigraphies. Basal sediments were always gray silty clays, succeeded upward by brown algal gyttja (Fig. 2). Magnetic susceptibility measurements confirmed visual inspection, showing no evidence along the sequences for changes (such as increases in eroded inorganic material) that might indicate a period of cooling. Radiocarbon age determinations (9, 10) allowed us to pinpoint sediments of the YDC in each core, and confirmed that there were no sedimentary changes during this period. Detailed tephrochronological analyses of these and other cores from the region (10), which include tephtras within the Last Glacial, confirm and support the radiocarbon chronology (11).

Forest development, determined from the pollen analyses (Figs. 3 and 4) (12), began about 14 ky BP with the arrival and increase of southern beech *Nothofagus*, probably *Nothofagus betuloides* (13). The landscape became completely forested as other trees followed (Fig. 3). The sequence of trees is broadly (*Tepualia* is the only exception) in

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accord with their modern latitudinal distributions: The earliest now extend furthest south (and hence are probably the most cold-tolerant), and later arrivals have more northerly southern limits (14–16), suggesting lower tolerance of cold climates. As additional species arrived, there were declines in the abundances of the earlier species (*Nothofagus*,

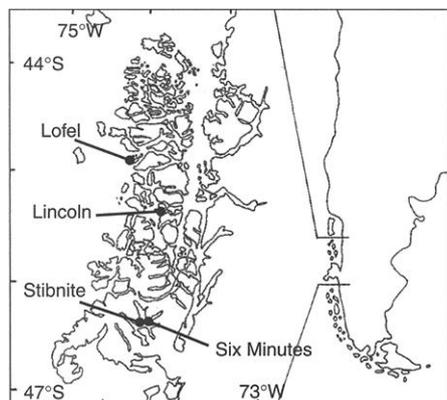


Fig. 1. Location maps of the study area within southern South America and of the sites within the study area. Laguna Lofel is located on Islas Chicas at 44°53.0'S 074°24.6'W, Laguna Lincoln on Isla Palumbo at 45°21.1'S 074°04.3'W, Laguna Six Minutes (36) on Taitao peninsula at 46°25.3'S 074°20.4'W, and Laguna Stibnite (9, 36) on Taitao peninsula at 46°26.7'S 074°25.1'W. All sites are between sea level and 50 m altitude.

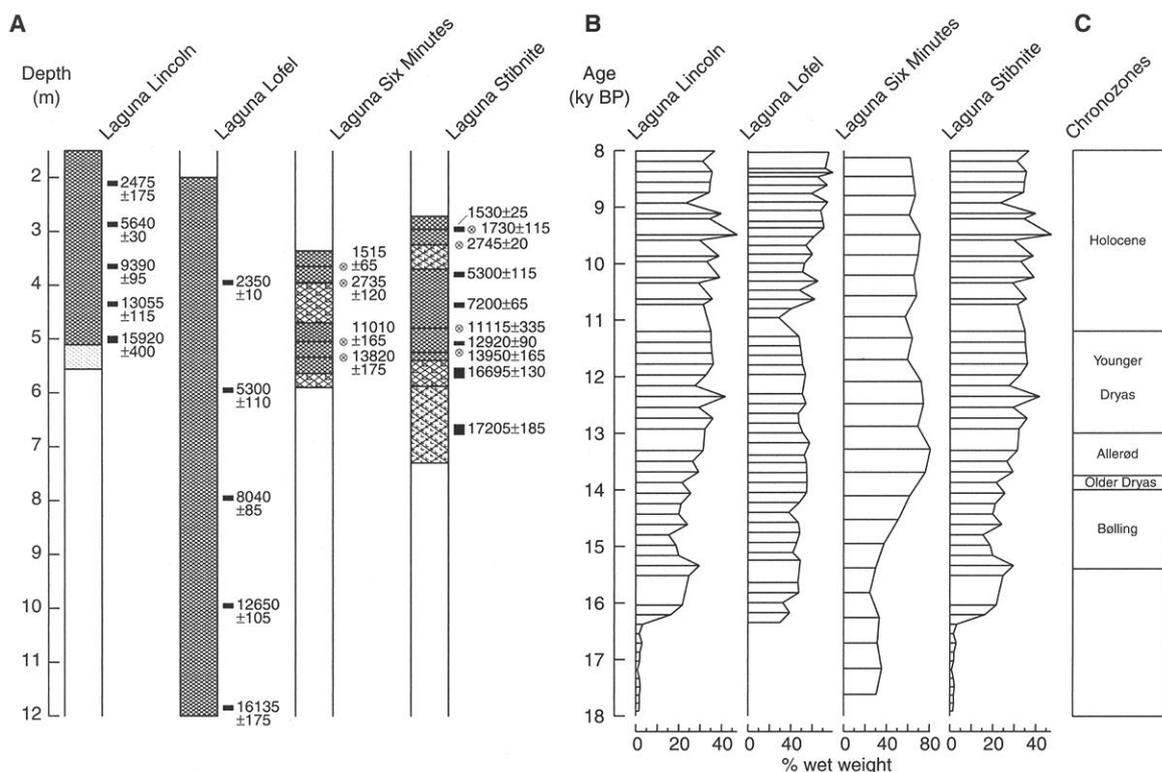
Pilgerodendron, and *Podocarpus*) as these were replaced in the forest, but the proportion of forest cover did not change significantly. There was little difference in the timing of arrival of the trees between the sites, except that *Weinmannia* increased later and was scarcer at more southerly sites (Fig. 4). Pollen analyses from within the YDC show no reversal of these trends of forest development, either to increasing abundances of nontree pollen types or to a reduction in abundance of any of the later trees. It is clear that at all sites, present interglacial conditions (in the sense of complete cover of temperate forest) started by 13 ky BP and were maintained from then onward.

Southern Chile has been a controversial area for the interpretation of events during the YDC (17–20). Part of the argument has been over the interpretation of sequences with complex stratigraphies, which are perhaps inevitable during a period of transition between a glacial and an interglacial. Another controversial area has been the timing of glacial readvances in the region (21). An extension of the Tronador ice cap during the YDC has been inferred from sedimentological evidence in proglacial Lake Mascardi, Argentina (41°S) (22). However, because modern glaciers of southern South America show behavior that is inconsistent in magnitude and direction (23), this single record cannot be taken as evidence of climate change. By focus-

ing on sequences of sediment located in stable parts of the landscape but receptive to, and preserving, input from a wide range of sources, our data show that the YDC was in fact a period of stable, or possibly slightly increasing, temperatures. This demonstration should make it possible to reinterpret and understand earlier investigations in southern Chile, while at the same time providing secure information on which to model temperature changes of the period seen elsewhere. The glacial readvance data may be better indications of locally varying precipitation change in the highly complex and varied topography of southern South America.

The data presented here from central southern Chile are in accord with evidence of the YDC from further south (18, 19) and north (24) and from New Zealand (25). The record from the meltwater channel infill at Canal de la Puntilla, Chile (41°S) (24) shows a major expansion of forest trees between 16.5 and 13 ky BP. The sequence has hiatuses and is complex stratigraphically, so a claimed cooling event after 13 ky BP is unsubstantiated. Records of methane from gas bubbles in Antarctic ice cores (26, 27) show that the Southern Hemisphere may have led the Northern Hemisphere into the interglacial by 2000 to 3000 years. Recent deuterium measurements from the Taylor Dome (28) and Vostok (29) Antarctic ice cores suggest a steady warming from 16 to 15 ky BP, reach-

Fig. 2. Stratigraphy and chronology. (A) Sediment stratigraphy and radiocarbon ages (uncalibrated) plotted against depth below the water surface for each of four sequences of lake sediments in southern Chile. Sediment stratigraphy follows the notation of Troels-Smith (37): Broadly, units with cross-hatching are organic gyttja, and other symbols indicate various inorganic components. Radiocarbon age determinations are indicated as conventional (black rectangles) or AMS (crossed circles). For the conventional determinations, the height of the block shows thickness of the sample. The core at Laguna Lofel ended on bedrock. (B) Loss-on-ignition values as a percentage of sediment wet weight for the sediments from the same four lakes, plotted against age in calendar years for the interval 8 to 18 ky BP. (C) Chronozones for the last glacial-interglacial transition, as defined by (32), converted to calendar years and plotted to the same scale as (B).



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ing full Holocene values by 11 ky BP, interrupted by the Antarctic Cold Reversal (ACR) (30) at 13.5 to 11.5 ky BP, and covering parts of both the cool YDC and the warmer northern European Allerød chronozone. These lines of evidence all agree in suggesting that the present interglacial began time-transgressively across the globe, beginning in the Southern Hemi-

sphere. Our pollen evidence shows no cooling contemporaneously with either the YDC or ACR, but it has long been known that pollen data, especially at times and places where subcontinental spread of trees has taken place, may lag climatic change by hundreds or even thousands of years (31). If the ACR was a general Southern Hemisphere phenomenon, it was

clearly not even strong enough to halt, and certainly not to reverse, forest development that had already begun. In contrast, climatic changes at mid- and high latitudes in the Northern Hemisphere during the YDC were sufficiently strong to halt and reverse forest development.

Fig. 3. Summary pollen stratigraphy plotted against age [calibrated (33)] below the water surface for each of four sequences of lake sediments in southern Chile. Black, pollen of trees; dark gray, pollen of herbs; light gray, spores of pteridophytes. Zonation schemes at right show chronozones (32), GRIP event stratigraphy (4), and the ACR (26).

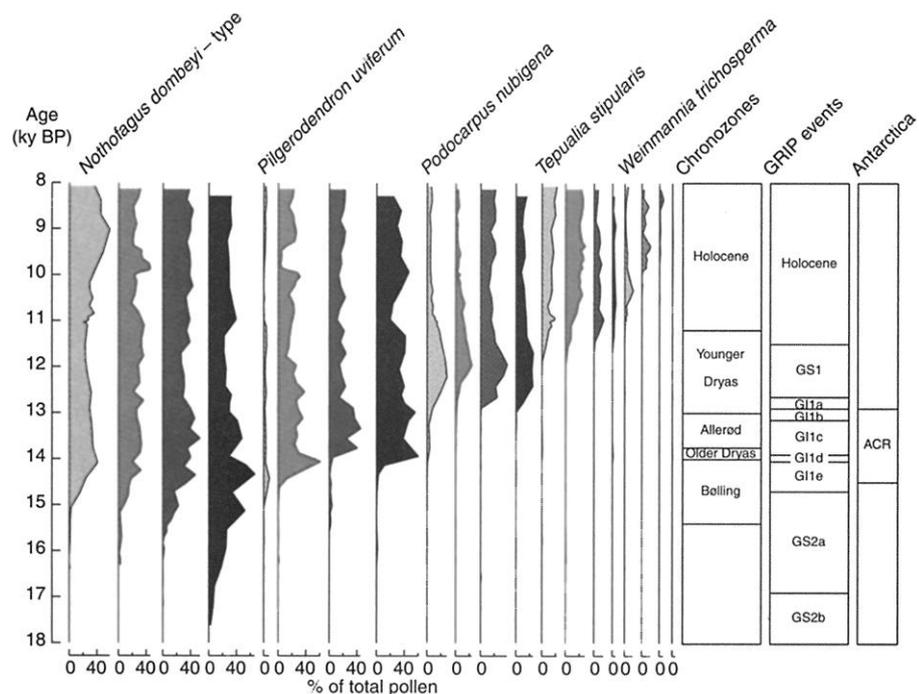
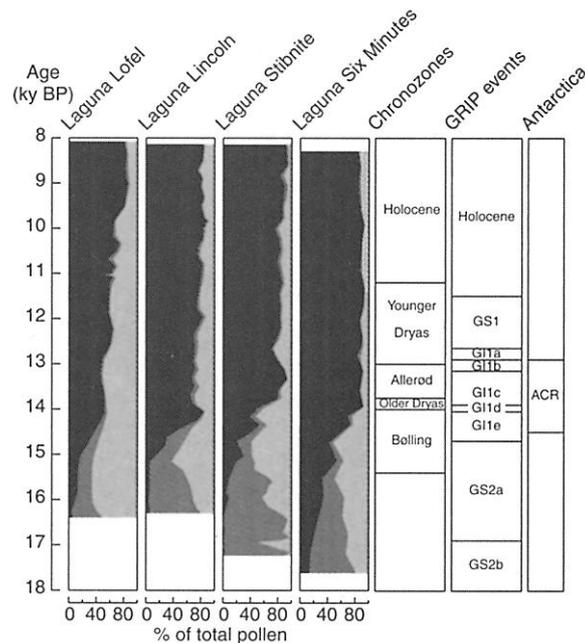


Fig. 4. Stratigraphy of main pollen taxa plotted against age [calibrated (33)] below the water surface for each of four sequences of lake sediments in southern Chile. For each taxon, sites are indicated by gray shading, from Laguna Lofel (palest), then Laguna Lincoln, Laguna Stibnite, and finally Laguna Six Minutes (black). Present southern limits for these taxa are as follows (14–16): *Nothofagus dombeyi*-type [seven Chilean species of *Nothofagus* (14)], 56°S; *Pilgerodendron uviferum*, 55°S; *Podocarpus nubigena*, 51°S; *Tepualia stipularis*, 53°S; and *Weinmannia trichosperma*, 49.5°S. Zonation schemes at right show chronozones (32), GRIP event stratigraphy (4), and the ACR (26).

References and Notes

1. The YDC is defined as 10 to 11 ¹⁴C ky BP by (32). This and all other age determinations have been converted to calendar years using CALIB 3.0 (33). Ages are expressed relative to the present, defined conventionally as 1950 A.D.
2. W. A. Watts, in *Studies in the Lateglacial of Northwest Europe*, J. J. Lowe, J. M. Gray, J. E. Robinson, Eds. (Pergamon, Oxford, 1980), pp. 1–21.
3. F. E. Mayle, L. C. Cwynar, *Quat. Sci. Rev.* **14**, 813 (1995).
4. S. Björck, et al., *J. Quat. Sci.* **13**, 283 (1998).
5. N. A. Stretten and J. W. Zillman, in *World Survey of Climatology, Volume 15, Climates of the Oceans*, H. van Loon, Ed. (Elsevier Amsterdam, 1984), pp. 263–429.
6. J. J. Lowe and M. J. C. Walker, *Trans. R. Soc. Edinb. Earth Sci.* **77**, 1 (1986).
7. I. L. Kristiansen, J. Mangerud, L. Lømo, *Rev. Palaeobot. Palynol.* **53**, 185 (1988).
8. V. Andrieu, C. C. Huang, M. O'Connell, A. Paus, *Quat. Sci. Rev.* **12**, 681 (1993).
9. S. H. Lumley and V. R. Switsur, *J. Quat. Sci.* **8**, 161 (1993).
10. S. G. Haberle and S. H. Lumley, *J. Volcanol. Geotherm. Res.* **84**, 239 (1998).
11. Radiocarbon determinations were made using both conventional and AMS techniques (as marked on Fig. 2) at the University of Cambridge Radiocarbon Laboratory (conventional) and the Arizona Accelerator Mass Spectrometry Laboratory and Beta Analytic, Inc. (both for AMS). All these determinations are listed in (10), and all determinations are consistent with each other, within and between dated series. All four basins are in impervious crystalline terrain. There is no limestone in the vicinity (34) and thus no reason to suspect that any of the determinations are affected by hardwater errors. Additionally, analyses of tephras in the sequences provide an independent chronology that is entirely consistent with that based on radiocarbon alone. Age-depth models for each site are presented in supplementary information (35).
12. Pollen data presented here are pollen percentage data, in order to most effectively display the changing proportions of forest and nonforest components of the vegetation and, secondarily, the changing proportions of tree types within the forested portion of the landscape. This data presentation is also the most straightforward for comparison with North Atlantic-region YDC pollen records. Pollen concentration and accumulation rate data are also available and provide information that complements the percentage data, supporting conclusions based on percentage data alone. Full pollen diagrams for all four sequences are presented in supplementary information (35).
13. C. Villagrán, P. Moreno, R. Villa, in *Ecología de los Bosques Nativos de Chile*, J. J. Armesto, C. Villagrán, M. K. Arroyo, Eds. (Editorial Universitaria, Universidad de Chile, Santiago, Chile, 1995), pp. 51–69.
14. C. J. Heusser, *Pollen and Spores of Chile* (Univ. of Arizona Press, Tucson, AZ, 1971).
15. D. M. Moore, *Flora of Tierra del Fuego* (Nelson, Oswestry, UK, 1983).
16. C. Marticorena and R. Rodríguez, Eds., *Flora de Chile Vol. I Pteridophyta—Gymnospermae* (Universidad de Concepción, Concepción, Chile, 1995).
17. C. J. Heusser, *Rev. Palaeobot. Palynol.* **65**, 9 (1990).
18. A. C. Ashworth, V. Markgraf, C. Villagrán, *J. Quat. Sci.* **6**, 279 (1991).
19. V. Markgraf, *Boreas* **20**, 63 (1991).
20. C. Clapperton, *Quaternary Geology and Geomorphology of South America* (Elsevier, Amsterdam, 1993).
21. G. Wenzens, *Quat. Res.* **51**, 238 (1999).
22. D. Ariztegui, M. M. Bianchi, J. Masferro, E. Lafargue, F. Niessen, *J. Quat. Sci.* **12**, 333 (1997).
23. L. Llibouty, in *Satellite Image Atlas of Glaciers of the*

- World: South America, R. S. Williams and J. G. Ferrigno, Eds., *U.S. Geol. Surv. Prof. Pap. 1386I* (1998), p. 148.
24. P. I. Moreno, T. V. Lowell, G. L. Jacobson, Jr., G. H. Denton, *Geogr. Ann.* **81A**, 285 (1999).
 25. C. Singer, J. Shulmeister, B. McLea, *Science* **281**, 812 (1998).
 26. T. Blunier et al., *Geophys. Res. Lett.* **24**, 2683 (1997).
 27. T. Blunier et al., *Nature* **394**, 739 (1998).
 28. E. J. Steig et al., *Science* **282**, 92 (1998).
 29. J. R. Petit et al., *Nature* **399**, 429 (1999).
 30. J. Jouzel et al., *Clim. Dynam.* **11**, 151 (1995).
 31. H. J. B. Birks, in *Climate and History: Studies in Past Climates and Their Impact on Man*, T. M. L. Wigley, M. J. Ingram, G. Farmer, Eds. (Cambridge Univ. Press, Cambridge, 1981), pp. 111–138.
 32. J. Mangerud, S. T. Andersen, B. E. Berglund, J. J. Donner, *Boreas* **3**, 109 (1974).
 33. M. Stuiver and P. J. Reimer, *Radiocarbon* **35**, 215 (1993).
 34. H. Niemeyer R., J. Skarmeta M., R. Fuenzalida P., W. Espinosa N., *Technical Report 60–61* (Servicio Nacional de Geología y Minería, Santiago, Chile, 1984).
 35. See Science Online for supplementary information, at www.sciencemag.org/feature/data/1053325.shl.
 36. S. H. Lumley, thesis, University of Cambridge (1993).
 37. J. Troels-Smith, *Danm. Geol. Unders. Raekke IV* **3(10)**, 73 (1955).
 38. We thank Corporación Nacional Forestal for permission to work in San Rafael and Las Guaitecas National Parks, Raleigh International and their staff and venturers for logistical help, the Natural Environment Research Council (NERC) and the Leverhulme Trust for financial support, R. Switsur and NERC for radiocarbon age determinations, J. Szeicz for help with fieldwork, A. Ashworth for comments on the manuscript, and J. Temple-Smith for technical help. K.D.B. initiated the project, K.D.B. and S.G.H. devised the paper, S.G.H. and S.H.L. obtained the tephrochronological data, K.D.B., S.G.H., and S.H.L. carried out fieldwork, and S.H.L. did the pollen and sediment analyses (with additional sediment analyses by J. Temple-Smith).

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A Niche Maintaining Germ Line Stem Cells in the *Drosophila* Ovary

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Stromal cells are thought to generate specific regulatory microenvironments or “niches” that control stem cell behavior. Characterizing stem cell niches in vivo remains an important goal that has been difficult to achieve. The individual ovarioles of the *Drosophila* ovary each contain about two germ line stem cells that maintain oocyte production. Here we show that anterior ovariole somatic cells comprising three cell types act as a germ line stem cell niche. Germ line stem cells lost by normal or induced differentiation are efficiently replaced, and the ability to repopulate the niche increases the functional lifetime of ovarioles in vivo. Our studies implicate one of the somatic cell types, the cap cells, as a key niche component.

Stem cells are defined by their ability to self-renew and to generate cell populations that differentiate to maintain adult tissues (1–3). Changes in stem cell behavior may contribute to aging and tumor formation, while stem cell populations will likely have therapeutic applications if their growth and differentiation can be controlled in vitro (4–6). However, their rarity and lack of distinctive characteristics make it difficult to study stem cells in their natural context within tissues. Stem cell behavior is thought to be controlled by neighboring stromal cells that create special microenvironments known as stem cell “niches” whose regulatory potential persists even when stem cells are absent. Until specific, individual niches can be identified and characterized, however, it will remain difficult to unravel their molecular regulatory mechanisms.

The *Drosophila* ovary is a tissue where stem cells can be studied at the cellular and molecular level in vivo (7, 8). Near the be-

ginning of each developing egg string (or ovariole) within the ovary reside about two germ line stem cells (GSCs) whose progeny differentiate into eggs within 8 days as they move at predictable rates along the ovariole. These stem cells are surrounded by three differentiated somatic cell types—terminal filament, cap, and inner sheath cells—that help make up an anatomically simple tubular structure known as the germarium (Fig. 1). GSCs are easily identified by size, location, and the shape of the fusome, an intracellular structure rich in membrane skeleton proteins. Stem cells usually contain a round fusome, but display a distinctive elongated fusome after division when they remain transiently connected with their daughter cell (9, 10). Under appropriate conditions, GSCs divide about once per day and are randomly lost by differentiation with a half-life of 4 to 5 weeks (11, 12). Recently, it was proposed that the somatic cells at the tip of the ovariole are organized into a niche that maintains and controls GSCs (12).

Ovariole anatomy is consistent with the existence of a niche at the anterior tip. After stem cell division, the daughter that lies closer to the terminal filament and cap cells remains a stem cell, whereas the daughter that more closely adjoins the inner sheath cells differentiates into a cystoblast (Fig. 1). Ana-

tomical asymmetry may ensure that equivalent stem cell daughters receive different fate-determining signals. GSCs require a signal mediated by Dpp, a homolog of human bone morphogenetic proteins 2 and 4, in order to remain as stem cells and to divide at a normal rate (12). Two other proteins needed to maintain GSCs, Piwi and Fs(1)Yb (Yb), act outside the germ line (13, 14). However, a requirement for intercellular signals does not by itself indicate the presence of a niche. A true niche should function independently of resident stem cells and be able to reprogram newly introduced cells to become stem cells. Consequently, we investigated whether the microenvironment at the ovariole tip can specify cells to become GSCs.

Ovarioles normally lose GSCs by differentiation, but the low rate of GSC loss and the possibility that rapid replacement quickly restores the original GSC configuration complicate observing such events. To study germaria with recently lost stem cells, we genetically marked and destabilized individual GSCs. We used FRT-mediated recombination (12) to generate mutant clones of *schurri* (*shn*), a gene we postulated would reduce GSC lifetime by disrupting *dpp* signaling (15, 16), under conditions where the mutant cells also lose an *armadillo-lacZ* marker (Fig. 2A). Because cystoblasts require 4 to 5 days to exit the germarium, the only remaining *lacZ*[−] cells 1 week after transiently activating the *hs-FLP* transgene by means of a heat shock will be clones consisting of *shn* mutant stem cells and their progeny of 4 to 5 days. With this marking system, marked *shn* GSCs that differentiate during the last 4.5 days can be recognized because *lacZ*[−] germ cells will remain in the germarium; moreover, the developmental age of the least mature such cell will indicate the elapsed time since GSC loss.

The results demonstrated that *shn* mutant stem cells are lost at an increased rate and are rapidly replaced by wild-type cells (17, 18). Seventy-nine germaria were found that retained *lacZ*[−] germ cells, revealing that a *shn* stem cell had been recently lost (Fig. 2, B and C). In every case they contained two wild-type stem cells, indicating that the lost *lacZ*[−] stem cell had been replaced by a wild-type stem cell. Even when the stem cell was lost so recently

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