a length scale of 200 km with a reduction in \( V_0 \), of only 2% (Fig. 3C, profile 3). By assigning different seismic velocities across the chemical interface, we find a \( V_0 \) decrease of almost 3% in a distance of 100 km, with half of the decrease occurring as an abrupt jump (Fig. 3C, profiles 1 and 2). For low Rayleigh number cases (10^3), similar structures are found but the chemical layer is embedded in a broad thermal halo (Fig. 3C, profile 4). We have not been able to find a purely thermal plume that produces an interface sharp enough to give the SKS multipathing; we conclude that it is more likely that the interface has a chemical origin.

The inclination of the interface is also diagnostic of the dynamics. If the dense basal layer is stable, then the interface between the two layers is always tilted toward the center of the anomaly (Fig. 3B). We find that the interface becomes tilted away from the central anomaly only when the chemical layer is unstable, that is, when the thermal buoyancy is greater than the chemical. Moreover, the two sides of the rising diapir are generally not parallel (as the seismic observations of Africa suggest); both sides become tilted inward near the base of the mantle and outward near the top of the diapir (Fig. 3A).

Alternatively, the inclination could be caused by a large-scale mode of convection, including flow associated with plate motion. Over the past 100 million years (My), Africa has moved northeastward in a hot spot of reference (15). This motion is in the same overall direction as the tilting of the ALVS (16). Although previous models have been able to reproduce the tilt of the ALVS, a tilt that may be caused by the shear associated with the African plate (17), they typically display diffuse mantle structures inconsistent with the sharpness implied by SKS multipathing. This result motivates a second class of dynamic models with an imposed velocity boundary condition simulating the northeastward motion of Africa (Fig. 3D through F). We find that the interface becomes tilted away from the central anomaly only when the chemical layer is unstable, that is, when the thermal buoyancy is greater than the chemical. Moreover, the two sides of the rising diapir are generally not parallel (as the seismic observations of Africa suggest); both sides become tilted inward near the base of the mantle and outward near the top of the diapir (Fig. 3A).

The inferred crystallographic class of circumstellar silicon carbide based on astrophysical infrared spectra is controversial. We have directly determined the polytype distribution of circumstellar SiC from transmission electron microscopy of presolar silicon carbide from the Murchison carbonaceous meteorite. Only two polytypes (of a possible several hundred) were observed: cubic 3C and hexagonal 2H silicon carbide and their intergrowths. We conclude that this structural simplicity is a direct consequence of the low pressures in circumstellar outflows and the corresponding low silicon carbide condensation temperatures.

**References and Notes**

10. See supporting online material on Science Online at www.sciencemag.org/cgi/content/full/296/5574/1850/DCC1.
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**Polytype Distribution in Circumstellar Silicon Carbide**

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The two most abundant forms of presolar silicon carbide are nanometer-sized diamond (1) and micrometer-sized diamond (2). Both are ubiquitous in primitive chondritic meteorites at 300 to 1800 parts per million (ppm) (diamond) and 1 to 28 ppm (SiC) (4). Silicon carbide is particularly interesting because it is known to form hundreds of different polytype structures in the laboratory, and the formation of a particular polytype is sensitive to growth conditions. Astronomical evidence of SiC in dusty envelopes of carbon stars comes from a relatively broad 13.3-μm infrared (IR) feature (5). However, attempts to distinguish from such IR spectra (6–9) whether α-SiC or β-SiC (10) predominates in carbon stars remain controversial (11–13).

Isotopic analysis of Si, C, and other elements in individual presolar SiC grains by ion microprobe shows that 99% of the SiC originated from low-mass asymptotic giant branch (AGB) stars of variable metallicity (with a small fraction possibly from stars of other chemical composition). Here, we assume that presolar SiC grains from primitive meteorites can be taken to be a representative sample of the grain contributions from all kinds of stellar
Presolar SiC was isolated from fragments of the matrix of the Murchison (CM2) carbonaceous chondrite that did not contain any fusion crust by acid dissolution and was separated into nine size fractions: KJA to KJI (17) (Fig. 1). We determined the distribution of SiC polytypes in the KJB fraction, which contained the highest SiC abundance (1.91 ppm of the bulk meteorite, corresponding to over 1/3 the mass of SiC) and highest purity (97% SiC) of the nine fractions (17). Furthermore, KJB is a representative sample of the presolar SiC population because 70% of the Murchison SiC population lies within 0.3 to 0.7 μm, characteristic of 90% of the grains in KJB. Secondary ion mass spectrometry (SIMS) measurements of individual SiC grains in KJH, KJG, KJF (18), KJE (19), KJC (20), and KJB (21) indicate that >99% are presolar grains. For transmission electron microscopy (TEM) microcharacterization of SiC grains sufficiently large for subsequent isotopic analysis by nanometer-scale SIMS (NanoSIMS), the Murchison KJE (90% between 0.7 and 1.6 μm) size fraction was also studied.

Analysis of grains along one zone axis (22) by selected area electron diffraction (SAED) and high-resolution TEM (HR-TEM) lattice imaging demonstrates unambiguously that only two SiC polytypes were present in KJB: cubic 3C β-SiC (Fig. 2) and hexagonal 2H α-SiC (Fig. 3) (10).

Intergrowths of these two polytypes were also observed. No other SiC polytypes were found among the 303 individual grains analyzed, with the exception of one 3C-2H SiC intergrowth grain containing many stacking faults and some short-range 4H order. Also, a small percentage of the heavily disordered grains were observed, which could not be identified as any polytype because they consisted of a random stacking of tetrahedral sheets.

Grains of 3C SiC were often multiply twinned with double diffraction present in SAED patterns, complicating polytype identification. One of the lowest energy interfaces in 3C SiC corresponds to twinning across {111} close-packed tetrahedral sheets. Twin boundaries in 3C SiC were predominantly of this type. Intergrowth grains contained variable proportions of 2H and 3C polytype order. As with 3C SiC single crystals, 3C SiC domains in intergrowth grains displayed a range of {111} twin microstructures and stacking fault densities. Each 3C SiC domain has four sets of <111> directions that can serve as an homoeptaxial growth interface to a 2H SiC domain, and nearly all intergrowth grains displayed one dominant 2H SiC orientation. Intergrowth grains often exhibited parallel 2H and 3C lamellae, but many contained only single large 2H and 3C domains. Electron diffraction and HR-TEM revealed no evidence of twinning in 2H SiC; however, stacking faults were observed.

Due to the large number of grains analyzed, it was impractical to identify their polytype other than from data along a single zone axis. Because of the finite tilt range of the TEM goniometer, a fraction of the randomly oriented grains will have no suitable zone axes (22) accessible. This fraction varies among SiC polytypes with distinctly different crystallographic symmetries (i.e., cubic, hexagonal, and rhombohedral). For example, there are 6 coplanar <1120> hexagonal directions lying in the (0001) plane compared with 12 <011> cubic directions isometrically distributed in three dimensions. Consequently, the fraction of grains that can be identified varies with crystal system, biasing TEM-measured polytype distributions. Nonetheless, the true distribution can be estimated.

The relation between the actual number of...
The occurrence of the 3C and 2H SiC polytypes (and their intergrowths) as predominant in presolar SiC grains can be understood in terms of thermochemical equilibrium calculations (29, 30). These predict that SiC condenses at \( \approx 1633 \) K for any C/O \( \approx 1.05 \) at pressures \( \approx 100 \) dyn/cm\(^2\) believed to be present in carbon star outflows (29, 30). Temperatures at which 2H SiC is known to grow and remain stable \((\approx 1473 \text{ to } 1723 \text{ K})\) fall within this range (24–26, 31, 32). In condensation experiments that synthesize 2H SiC, formation of predominantly 3C SiC is observed at approximately \( > 1700 \) K (31). A range of formation temperatures is reported in the literature for the different SiC polytypes. However, a phase diagram of polytype formation cannot be readily deduced from these studies because different processes are used to synthesize SiC and many experimental parameters vary. The most pertinent data are found in studies that examine the relative temperature dependence of several polytypes synthesized by a given process in which only a few experimental parameters are varied. A detailed review of the available literature on such studies indicates that all higher order SiC polytypes form at temperatures greater than that of 3C SiC under similar conditions for a given vapor condensation process (31). This explains why only two (2H and 3C) out of \( \geq 250 \) possible polytypes are observed in circumstellar SiC.

The hypothesis suggested is that, close to carbon stars, photon and particle irradiation as well as temperatures are sufficiently high to prevent nascent nucleating clusters from reaching critical size for sustained growth. A in radii in carbon star atmospheres, where irradiation and temperatures are sufficiently low, the highest temperature condensates, such as graphite and TiC, can form (30). At larger radii, the highest temperature SiC polytype observed, 3C, can condense. At still larger radii, in expanded cooler gas regions, the lower temperature 2H SiC can form. Thus, we infer that intergrowth grains probably formed at radii intermediate to the regions of predominantly 3C and 2H SiC formation. In particular, 2H SiC heteropelitic growth could occur on preexisting 3C SiC grains that were formed at smaller radii and transported by radiation pressure to cooler regions at larger radii.

**Table 1.** Murchison KJB SiC polytype distribution, based on TEM characterization of 303 grains, corresponding to \( > 90 \% \) of the total grains examined. Included are those grains that, upon tilting, were found to be actually two grains randomly stuck together and those with no suitable zone axes within the goniometer tilt limits. The errors reflect the greater of sampling errors or the propagated uncertainties in \( \varepsilon_i \) for each grain. The uncertainties in \( \varepsilon_i \) for a grain result from uncertainties in determining the twin and intergrowth microstructure because not all 3C \( \approx 111 \) twin planes, e.g., the inclined twin planes, are visible. In intergrowth grains, only those 2H domains associated with edge-on 3C \( \approx 111 \) planes will be visible.

<table>
<thead>
<tr>
<th>Grain type</th>
<th>Population (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>3C</td>
<td>80.03 ± 2.38</td>
</tr>
<tr>
<td>2H/3C intergrowths</td>
<td>16.86 ± 4.07</td>
</tr>
<tr>
<td>2H</td>
<td>2.08 ± 0.52</td>
</tr>
<tr>
<td>Disordered</td>
<td>1.04 ± 0.33</td>
</tr>
<tr>
<td>All other polytypes</td>
<td>&lt; 0.33</td>
</tr>
</tbody>
</table>

**Fig. 4.** NanoSIMS (A) secondary electron image and (B and C) isotopic ratio maps of \( ^{12}\text{C}/^{13}\text{C} \) and \( ^{14}\text{N}/^{15}\text{N} \), respectively, for the presolar 2H \( \alpha\)-SiC shown in Fig. 3. Scale bar, 1 \( \mu\text{m} \).

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References and Notes

10. In the notation described by L. S. Ramsdell [Am. Mineral. 32, 64 (1947)], a polytype is denoted by the number of tetrahedral sheets in the unit cell followed by C, H, or R, representing crystal symmetry (i.e., cubic, hexagonal, or rhombohedral). The only cubic SiC polytype, 3C, is known as α-SiC, and all other SiC polytypes are known collectively as α-SiC.
Germline Stem Cells Anchored by Adherens Junctions in the Drosophila Ovary Niches

Xiaqing Song, Chun-Hong Zhu, Chuong Doan, Ting Xie*

How stem cells are recruited to and maintained in their niches is crucial to understanding their regulation and use in regenerative medicine. Here, we demonstrate that DE-cadherin-mediated cell adhesion is required for anchoring germline stem cells (GSCs) in their niches in the Drosophila ovary. Two major components of this adhesion process, DE-cadherin and Armadillo/β-catenin, accumulate at high levels in the junctions between GSCs and cap cells, one of the niche components. Removal of these proteins from GSCs results in stem cell loss. Furthermore, DE-cadherin is required for recruiting GSCs to their niche. Our study demonstrates that anchorage of GSCs in their niche by DE-cadherin-mediated adhesion is important for stem cell maintenance and function.

Stem cells exist in many adult tissues and are responsible for generating differentiated cells that replace cells lost during an animal’s lifetime (1–3). Understanding the molecular mechanisms controlling stem cell function in vivo is crucial to the future use of stem cells in regenerative medicine, as well as in understanding aging, tumor formation, and degenerative diseases (4–6). GSCs in the adult Drosophila ovary are an excellent system in which to study stem cell and niche function in vivo (7, 8). At the tip of the gerarium (Fig. 1A), located at the tip of each ovariolar ovary, a niche exists for two or three GSCs whose progeny eventually develop into mature oocytes (9–12). GSCs can be reliably identified based on size, location, and the shape of their fusome. Stem cells contain fusomes (also known as spectrosomes) that are usually round but can be elongated in shape while transiently connected to their daughter cells after division (13, 14). These stem cells directly contact cap cells and are close to two other somatic cell types: terminal filament cells and inner germarial sheath cells. Terminal filament cells and cap cells express the genes decapentaplegic (dpp), fs(1)Yb (Yb), piwi, and hedgehog (hh), which are known to be important for GSC maintenance (9–12).

Cell adhesion mediated by DE-cadherin, a Drosophila classic cadherin encoded by the shotgun (shg) and Armadillo (Arm), the Drosophila β-catenin homolog, plays an important role between germ cells and follicle cells during oogenesis (15–19). To determine whether DE-cadherin-mediated cell adhesion is important for anchoring GSCs in their niche, we first examined the expression of DE-cadherin and Arm proteins in the gerarium. The hh-lacZ line, in which the bacterial lacZ gene with a basal promoter is inserted into the hh gene, was used to identify cap cells and terminal filament cells (20). These germaria were also immunostained for Hu-ⅡⅡ (Hs) and/or Vasa proteins, molecular markers for the fusomes and germline cells, respectively (21, 22). DE-cadherin protein, immunolocalized at high levels as a single band in the interfaces between cap cells and GSCs (Fig. 1B). With more detergent than used in the normal procedure (23), the DE-cadherin band separated into two bands just

between cap cells and GSCs (Fig. 1C). DE-cadherin is a membrane-associated protein, which accumulates on the membranes of cap cells and GSCs. Arm and DE-cadherin colocalized in these sites (Fig. 1D to F). Note that the distribution of these proteins was not uniform in the contact areas between GSCs and cap cells or between cap cells themselves. Instead, there were focal sites between the cells that were rich in DE-cadherin and Arm proteins (Fig. 1F), possibly representing adherens junctions. Consistent with this idea, typical adherens junctions were observed between cap cells and GSCs (Fig. 1G), suggesting that DE-cadherin-mediated cell adhesion between cap cells and GSCs in the form of adherens junctions may be involved in anchoring GSCs to cap cells.

To investigate whether DE-cadherin-mediated cell adhesion is essential for maintaining GSCs in their niche, we used FLP-mediated recombination of the FLP recombination target sequences (FRTs) (24, 25) to produce marked GSCs that lack functional copies of either shg or arm (23). The marked GSCs were identified by their loss of expression of lacZ (9). To investigate whether the removal of DE-cadherin from GSCs disrupts its accumulation in the contact sites, we used the deletion allele of Shg, shgΔ2089, to remove DE-cadherin proteins from GSCs in the adult ovary (15). With this allele, DE-cadherin accumulation diminished in the interfaces between GSCs and cap cells within 1 week (Fig. 2, A and B). Partial depletion was observed in some cases, which may be due to the persistence of the protein (Fig. 2A). In the germaria containing shgΔ2089 GSCs, the accumulation of DE-cadherin was maintained between wild-type GSCs and cap cells.

To further determine the importance of DE-cadherin-mediated adhesion in maintaining GSCs in their niche, we used two shg alleles: the deletion allele (shgΔ2089) and a weak allele (shgΔ2089 Δ23). Consistent with the prediction that the adhesion is important for anchoring GSCs, mutant shgΔ2089 GSCs were lost very quickly (with a half-life of 0.8 weeks), causing marked shgΔ2089 GSCs to occur at a much lower frequency in germaria during the first week after

R E P O R T S

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