13. P. M. Tucker, H. J. Yorston, *Pitfalls in Seismic Interpretation*, J. C. Hollister, Ed. (Society of Exploration Geophysicists, Tulsa, OK, 1973).
14. L. E. Peters *et al.*, *J. Geophys. Res.* **111**, B01302 (2006).
15. B. Kamb, *The West Antarctic Ice Sheet: Behavior and Environment*, R. B. Alley, R. A. Bindschadler, Eds. (American Geophysical Union, Washington, DC, 2001), pp. 157–200.
16. The phase of the reflection from the base of the till is diagnostic of porosity, with reflection phase angles ranging from 70° to 120° for porosity ϕ from 45 to 15%, respectively. However, our instrument was not phase sensitive; future work with a phase-sensitive radar or with seismic experiments would determine this property.
17. H. Conway, B. L. Hall, G. H. Denton, *Science* **286**, 280 (1999).
18. S. Shipp, J. B. Anderson, E. W. Domack, *Geol. Soc. Am. Bull.* **111**, 1486 (1999).
19. A. B. Mosola, J. B. Anderson, *Quat. Sci. Rev.* **25**, 2177 (2006).
20. E. Domack, E. Jacobson, S. Shipp, J. Anderson, *Geol. Soc. Am. Bull.* **111**, 1517 (1999).
21. D. Blankenship, S. Rooney, R. Alley, C. Bentley, *Ann. Glaciol.* **12**, 200 (1989).
22. B. Hallet, L. Hunter, J. Bogen, *Global Planet. Change* **12**, 213 (1996).
23. Similar or somewhat larger sediment fluxes are indicated by the geometry and likely time for deposition of the grounding-zone wedges described by Mosola and Anderson (*19*), which is consistent with the ice sheet having expanded over easily eroded, poorly consolidated sediments of the Ross Sea.
24. P. Christoffersen, S. Tulaczyk, F. D. Carsey, A. E. Behar, *J. Geophys. Res.* **111**, F01017 (2006).
25. D. M. Holland, S. S. Jacobs, A. Jenkins, *Antarct. Sci.* **15**, 13 (2003).
26. H. Engelhardt, W. B. Kamb, *J. Glaciol.* **44**, 223 (1998).
27. N. R. Iverson, T. S. Hooyer, R. W. Baker, *J. Glaciol.* **44**, 634 (1998).
28. R. B. Alley, *Deformation of Glacial Materials*, A. J. Maltman, B. Hubbard, M. J. Hambrey, Eds. (Special Publication 176, Geological Society of London, 2000), pp. 171–179.
29. P. N. Sen, C. Scala, M. H. Cohen, *Geophysics* **46**, 781 (1981).
30. We thank D. Voigt, I. Joughin, P. Winberry, L. Peters, B. Bindschadler, and P. Burkett for their help; and University Navstar Consortium (UNAVCO), Raytheon Polar Services, and Kenn Borek Air for logistical support. Partial support was provided by NSF through grant numbers 0229629, 0226535, 0424589, 0440447, 0440899, 0447235, 0531211, and 0539578, and by the Gary Comer Science and Education Foundation.

Supporting Online Material
www.sciencemag.org/cgi/content/full/1138393/DC1
Fig. S1

4 December 2006; accepted 21 February 2007
Published online 1 March 2007;
10.1126/science.1138393
Include this information when citing this paper.

Effect of Sedimentation on Ice-Sheet Grounding-Line Stability

**Richard B. Alley,[1]* Sridhar Anandakrishnan,[1] Todd K. Dupont,[1,2]
Byron R. Parizek,[1,3] David Pollard[1]**

Sedimentation filling space beneath ice shelves helps to stabilize ice sheets against grounding-line retreat in response to a rise in relative sea level of at least several meters. Recent Antarctic changes thus cannot be attributed to sea-level rise, strengthening earlier interpretations that warming has driven ice-sheet mass loss. Large sea-level rise, such as the $\approx$100-meter rise at the end of the last ice age, may overwhelm the stabilizing feedback from sedimentation, but smaller sea-level changes are unlikely to have synchronized the behavior of ice sheets in the past.

Ice sheets both cause and respond to sea-level changes. Large, rapid ice-sheet fluctuations have occurred in the past (*1*) and may recur, but the relative importance of different causes remains uncertain. Here we show that sedimentation beneath ice shelves at grounding lines (where ice begins to float) provides substantial stability against ice-sheet advance or retreat during sea-level changes of up to a few meters or more. Such forcing from sea-level change occurs on the same time scale as does sedimentary stabilization, pointing to other environmental controls as being especially important to ice sheets.

In 1905, R. F. Scott reported evidence of the geologically recent shrinkage of the Antarctic Ice Sheet, despite persistently cold conditions (*2*). Scott suggested that more snowfall in a warmer past explained the larger ice sheet at that time. Subsequent evidence showing the (near)synchrony of northern and southern ice retreat after the last ice age and that Antarctica had experienced larger ice sheets when the southern climate was colder and drier disproved Scott's hypothesis.

Many workers (*3*) instead came to accept Penck's argument that sea-level rise from the melting of northern ice sheets had driven the Antarctic ice to retreat (*4*). Ice-sheet synchronization by smaller sea-level changes linked to Heinrich events or other millennial events has also been frequently proposed (*1*). However, simple sea-level control is inconsistent with sparse data indicating that, after an initial retreat from the outer shelf (*5*), additional Antarctic shrinkage was delayed until near the end of the northern-driven deglacial sea-level rise (*6*). Sea-level control is also inconsistent with the observed slowing of Antarctic ice-stream motion in response to rising tide (*7*, *8*).

Sedimentary stabilization of nonfloating tidewater glaciers is well known (*9*): Tall, steep-sided sediment bodies deposited between ice and water reduce iceberg calving. Ice flowing from large ice sheets more typically forms floating ice shelves, with sediment being deposited beneath the gradually sloping ice-shelf base. Our model results and the observations of (*10*) show that such sedimentation also serves to stabilize the grounding line and thus to prevent ice-sheet shrinkage in response to a small ($<\approx$10 m) sea-level rise. Penck's hypothesis (*4*) may still be valid for ice-sheet response to a larger sea-level rise ($\approx$100 m); however, our results, together with recent evidence that ice shelves respond sensitively to ocean temperature changes and quickly propagate the response inland (*11*), point to the greater importance of other environmental variables, especially sub–ice-shelf temperature.

Going from the grounded West Antarctic Ice Sheet to the floating Ross Ice Shelf, the upper surface typically drops $\approx$10 to 25 m in a ramp extending over a few kilometers, which is much steeper than the slope upglacier or downglacier (*12*). Where data are available, this surface-elevation drop is not caused by thinning of the ice, as might occur from strong basal melting near the grounding line, nor from the effects of basal crevassing or near-surface density changes (*12*). Instead, the surface-elevation ramp results mainly from a corresponding ramp in basal topography. Thus, the onset of flotation is not caused primarily by a downglacier thinning of ice to the flotation criterion, but more by a downglacier drop in the elevation of the glacier bed. This contributes to the observed stability of the grounding-line position over many decades (*12*) and to the ice-stream slowdown in response to rising tide (*7*, *8*).

Available data indicate that the topographic step in the glacier bed was formed by the recent deposition of primarily subglacially transported sediment. As shown in (*10*), a sediment wedge occurs just upglacier of the grounding line of Whillans Ice Stream, and this wedge is remarkably similar to the numerous till-dominated deposits formed at the grounding line of the extended ice sheet during its retreat from the continental-shelf edge as the last ice age ended (*13*). Observations are available from beneath the grounded portions of two active ice streams (Whillans and Bindschadler) feeding the Ross Ice Shelf, and both showed deformation of soft tills (*14*); although the deformation is probably discontinuous in space and time (*14*), notable sediment transport results. The geology near the grounding zone of the Ross Ice Shelf has not been mapped in detail, but available data indicate that the ice flows along fault-controlled basins containing poorly consolidated Tertiary and perhaps Quaternary sediments (*15*). It is highly unlikely that the sedimentary

---

[1]Department of Geosciences and Earth and Environmental Systems Institute, Pennsylvania State University, University Park, PA 16802, USA. [2]Department of Earth and Environmental Sciences, University of Illinois at Chicago, Chicago, IL 60607, USA. [3]Department of Physics, The College of New Jersey, Ewing, NJ 08628, USA.

*To whom correspondence should be addressed. E-mail: rba6@psu.edu

deposit discovered by Anandakrishnan *et al.* (*10*) is a localized feature and that the topographic step is caused by an unknown transverse geologic structure extending across the entire Ross Ice Shelf, except where surveyed by Anandakrishnan *et al.* (*10*). Instead, sedimentary control of most or all of the grounding line is highly likely, with the available data supporting wedge formation within the troughs of modern and past ice streams (*13*).

Using three different ice-flow models [labeled Dt (Dupont), Pk (Parizek), and Pd (Pollard) for their lead developers (*11*, *16, 17*)] including longitudinal as well as basal shear stresses, we have assessed the effect of sub–ice-shelf sedimentation on an ice-stream/ice-shelf system. The models were run for a coupled ice-stream/ice-shelf configuration approximating Whillans Ice Stream and the adjacent Ross Ice Shelf across the grounding-zone wedge. In some runs, ice-shelf buttressing was prescribed, offsetting much of the spreading tendency at the grounding line. After reaching a steady state with a flat bed, the model ice-stream/ice-shelf system was perturbed by instantaneously adding a wedge of sediment similar to the 31-m-high wedge observed by Anandakrishnan *et al.* (*10*), with the same basal friction as beneath the preexisting ice stream (*18*). The evolution to a new steady state was assessed while the geometry of the sediment wedge was held constant. The response of steady-state configurations to instantaneous sea-level change was simulated with and without grounding-zone wedges.

The frictional drag from increased ice/sediment contact with the addition of the wedge slows and thickens the ice above, which in turn causes the geometric effect of the wedge to become important and to further restrict the ice flow (Fig. 1). The resulting grounding-line advance beyond the crest of the wedge causes flotation to occur where the bed falls away, matching observations at the modern grounding line, whereas without the wedge, flotation occurs where the ice thins sufficiently.

In all of our models, sea-level rise in the absence of a wedge causes the grounding line to retreat from its initial position because the reduction in basal friction from the flotation of previously grounded ice is more important than the increase in back pressure from the deeper water. The wedge causes the ice above the wedge crest to thicken to well above the flotation level; small instantaneous sea-level rise then causes very small grounding-line retreat to a new position that still lies beyond the crest of the wedge and well beyond the no-wedge position. Larger sea-level rise (≈5 m or more) causes the ice to float free of the wedge and to reach the same steady state as in the no-wedge case (Figs. 1 and 2).

Larger wedges have greater ice thickness above flotation levels at the wedge crest and so require larger sea-level rise to force the grounding line upglacier of the wedge crest. However, as shown in Fig. 3, the dependence of the resistance on the wedge height or length is steeper for smaller wedges than for larger ones. Furthermore, if the wedge volume grows at a constant rate, the wedge height and length will increase more rapidly at first and more slowly later. Both effects combine to produce a more rapid increase in resistance at early stages of growth than at later stages (*19*).

Stiffer wedges (those with greater frictional resistance for a given basal velocity) also require larger sea-level rise to force the grounding line upglacier of the wedge crest (Fig. 2). We expect that at least portions of a wedge will often be stiffer than the surrounding no-wedge regions. The steepened ice/air surface slope that develops in response to friction from a wedge (Figs. 1 and 4) will steepen the subglacial hydrologic-potential gradient and speed the flow of subglacial water, reducing water storage and pressure and thus reducing the lubrication of ice motion by sliding or till deformation (*20*). Consideration of our numerical experiments with stiffer wedges and of the additional stabilizing effect that would occur from sedimentation during sea-level rise at ordinary rates suggests to us that a sea-level rise of >≈10 m may be required to force retreat from the wedge deposited beneath Whillans Ice Stream over the past millennium or so (*10*).

Additional simulations of grounding-line/wedge interactions reveal a rich range of behavior

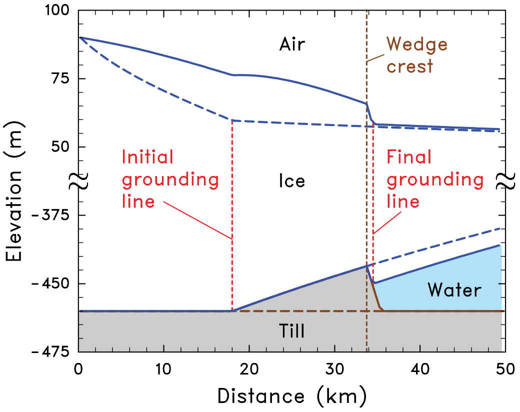

Fig. 1. Effect of grounding-line deposition (Pd model). Dashed lines show the steady ice-stream profile in the absence of a grounding-line wedge, and solid lines show the wedge and the corresponding steady ice-stream profile. The wedge causes the ice to thicken, the grounding line to advance past the crest of the wedge, and an inflection point to form in the upper surface at the upglacier end of the wedge, which might serve to increase water storage there.

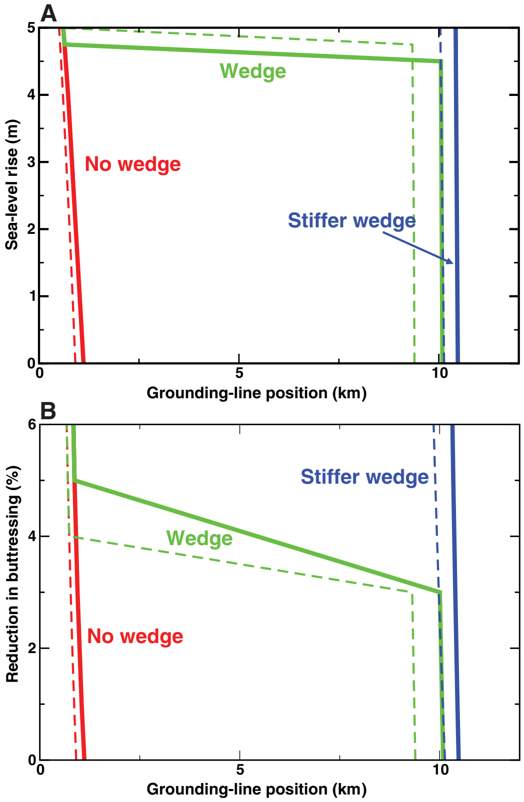

Fig. 2. Grounding-line stability in the Pk (solid lines) and Dt (dashed lines) models. Ice flows from left to right. In the absence of a wedge, the grounding line is at 1.1 km on this scale. The Pk and Dt experiments are not identical because of effects of the underlying model physics on the ice-shelf and wedge geometry, but the experiments are roughly comparable, and the results are clearly qualitatively identical and quantitatively similar. The ability of the grounding line to retreat is greatly limited by the constant-thickness boundary condition at the upglacier (left) end of the model domain; additional experiments with the same boundary condition applied farther away from the grounding line show much greater sensitivity to perturbations when the grounding line is upglacier of the wedge, and they emphasize the stabilizing influence of the wedge. (**A**) Response to sea-level rise. Adding the wedge moves the grounding line to 10.1 km, and increasing the stiffness of the wedge (the frictional resistance for a specified sliding velocity) by an order of magnitude moves the grounding line to 10.5 km. Sea-level rise causes retreat in all cases. However, the wedge causes the grounding-line retreat to be small up to some limit, beyond which the behavior is identical to the no-wedge case. The stiffer wedge requires a higher sea-level rise to reach that limit. (**B**) Response to a reduction in buttressing. Initial buttressing opposes 69% of the spreading tendency of the ice shelf at the grounding line. A 6% reduction means that buttressing opposes 0.94 × 69% = 65% of the spreading tendency. A reduction of ≈25% is required to cause retreat from the stiffer wedge.

(Fig. 4). Steady grounding-line positions on the upglacier side of a wedge were not simulated, consistent with the theory that such solutions are unstable (*21*). Migration of the grounding line across an otherwise horizontal bed is strongly influenced by any wedges encountered (*22*). The advance of the grounding line to a wedge crest is accelerated, but advance beyond the wedge crest slows relative to the no-wedge case. Similarly, the grounding line lingers on the downglacier side of a wedge during retreat and then races off of the upglacier edge. Under some circumstances, an advancing ice shelf has a more gradual basal slope than the upglacier side of a wedge, causing ice to bridge across water and ground on the wedge top, with the possibility of trapping water subglacially if the transverse geometry is favorable (*23*).

Our models show that the thickening of overlying ice in response to sedimentation stabilizes the grounding-line position against sea-level rise or buttressing reduction, and we infer that the extra thickness will tend to stabilize against any other environmental perturbation. Even a few centuries of sedimentation typically should provide stability against sudden sea-level rise from an outburst flood or surge of plausible-magnitude from another ice sheet, so sea-level change that is sufficiently large to control grounding-line positions will typically occur through noncatastrophic processes at usual rates (on the order of 1 cm/year or less) over several hundred to thousands of years. An ice-thickness change of ≈1.1 m has the same effect on grounding-line flotation as does a sea-level rise of 1 m, but this effect can be achieved more rapidly through sustained changes in snowfall or temperature. (Although slight warming causes very little surface melting in cold places, such as Whillans Ice Stream, a 1°C change can increase the surface melt rate by many tens of centimeters per year in warmer regions, such as some south-Greenland outlet glaciers.)

Changes in ice-shelf buttressing may be especially effective in overcoming the stabilizing effect of grounding-line sedimentation. As shown in Fig. 2, a 5% reduction in buttressing has about the same influence on the grounding line as does a 5-m rise in sea level for our reference case. A 5-m sea-level rise requires 500 years at the typical rate of the last deglaciation and 2500 years at 20th-century rates. Under some circumstances, a 5% decrease in buttressing will be achieved by an ≈5% decrease in the ice-shelf area generating side drag (*24*, *25*). Because the basal melt rate of ice shelves is observed to increase with water temperature by ~10 m $\text{year}^{-1}\,{}^\circ\text{C}^{-1}$ (*26*), even a fairly subtle perturbation in water temperature can cause a change of >5% in buttressing over years or decades. As an extreme example, a much larger change occurred in a few weeks during 2002 for the Larsen B Ice Shelf (*27*).

Grounding-zone sedimentation appears to be widespread to ubiquitous under major ice streams that control ice sheets (*28, 29*). Any near-stillstand of a grounding line (from an encounter with a preexisting basal high or narrowing of a trough or from time changes in basal lubrication, ice-shelf melting, or other environmental conditions) will be stabilized by sedimentation, except under special circumstances. In turn, because of spatial variability in sedimentation rates and physiographic variations between ice-stream troughs, any grounding-line retreats that are forced by sea-level rise are likely to be asynchronous for different ice sheets or different sectors of a large ice sheet.

Penck's hypothesis that Northern Hemisphere ice-sheet melting drove Antarctic ice-sheet retreat at the end of the ice age (*4*) may be accurate [also see (30)], with the delay in Antarctic retreat after the onset of sea-level rise being linked to sedimentary dynamics. Although our results indicate that sea-level changes of a few meters are unlikely to substantially affect ice-sheet behavior, 100-m changes should have considerable effects. However, sea level may exert the primary control on the ice sheet only if there is multimillennial stability in the other variables that affect ice sheets more quickly, such as water temperature under ice shelves. Because oceanic temperature probably changed with the deglaciation, perhaps linked to the return of North Atlantic Deep Water to the Southern Ocean (*31*), we consider it possible that ice-shelf changes contributed to or even dominated grounding-line retreat in some sectors of the ice sheet. Regardless, our results show that synchronous behavior of ice sheets with active sedimentary systems on millennial time scales is unlikely to indicate ice-sheet teleconnections via sea level and instead probably indicates common climatic forcing, which demonstrably can have very large and rapid effects on ice sheets.

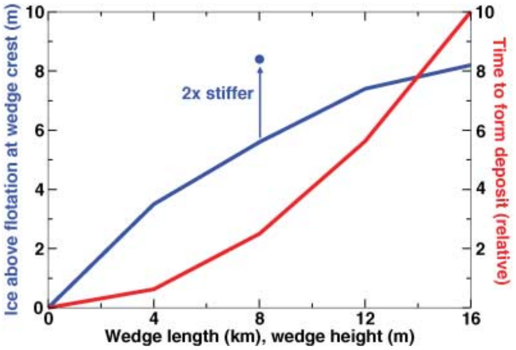

Fig. 3. Effect of wedge height on resistance to grounding-line retreat (blue) and on the time required for wedge deposition (red) in the Pd model. In this case, simulations were run for wedges having an upglacier slope of 0.001, a downglacier slope of 0.01, and heights of 0, 4, 8, 12, and 16 m with corresponding lengths of 0, 4, 8, 12, and 16 km, respectively. The thickness of ice above the wedge crest, which provides the resistance to grounding-line retreat, increases with wedge size; however, the increase in ice height above the flotation level is slower than the increase in wedge height, so earlier increments of wedge growth are more effective at stabilizing the grounding line, especially as successive height increments take longer to form if the sediment supply is constant. (The time depends on the sediment flux and so is plotted in relative units.) In comparison, the effect of doubling the stiffness of an 8-km wedge is also indicated. Similar experiments in the Dt model yield comparable trends but somewhat smaller height above the flotation level.

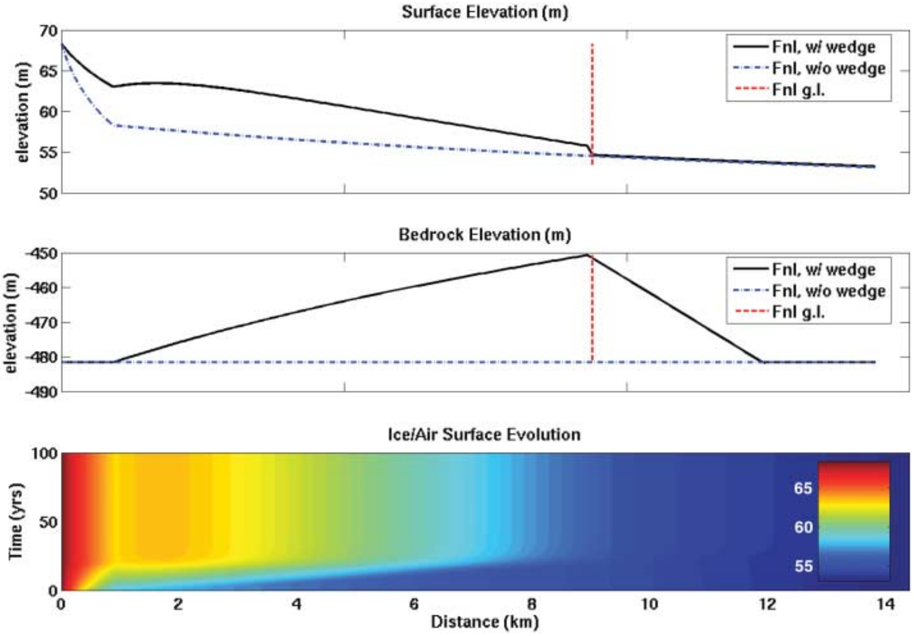

Fig. 4. Time-dependent response to instantaneous insertion of a wedge (Dt model). The final (Fnl.) geometries of the surface and bed are shown at the top, and the ice/air surface elevation (in meters) as a function of time and distance is color-coded. Ice thickness was held constant at the upglacier end (0 km, left). Most of the response to the insertion of the wedge was completed in ≈20 years.

References and Notes

1. M. Elliot *et al.*, *Paleoceanography* **13**, 433 (1998).
2. R. F. Scott, *Geogr. J.* **25**, 353 (1905).
3. J. T. Hollin, *J. Glaciol.* **32**, 173 (1962).
4. A. Penck, *Sitzungsber. Preuss. Akad. Wiss. Berlin Phys.-Math. Kl.* **6**, 76 (1928).
5. J. B. Anderson, S. S. Shipp, A. L. Lowe, J. S. Wellner, A. B. Mosola, *Quat. Sci. Rev.* **21**, 49 (2002).
6. H. Conway, B. L. Hall, G. H. Denton, A. M. Gades, E. D. Waddington, *Science* **286**, 280 (1999).
7. S. Anandakrishnan, D. E. Voigt, R. B. Alley, M. A. King, *Geophys. Res. Lett.* **30**, 1361 (2003).
8. The increase in pressure opposing ice flow from the rising tide is more important than the decrease in basal friction as the rising tide floats ice off of its bed, contrary to the expectation of the simplest model, in which the spreading tendency of grounded (nonfloating) ice is restrained by basal friction. If the forcing and the resulting slowdown were sustained, thickening and grounding-line advance would result from the sea-level rise.
9. M. Meier, A. Post, *J. Geophys. Res.* **92**, 9051 (1987).
10. S. Anandakrishnan, G. A. Catania, R. B. Alley, H. J. Horgan, *Science* **315**, 1835 (2007); published online 1 March 2007 (10.1126/science.1138393).
11. T. K. Dupont, R. B. Alley, *Geophys. Res. Lett.* **32**, L04503 (2005).
12. H. J. Horgan, S. Anandakrishnan, *Geophys. Res. Lett.* **33**, L18502 (2006).
13. A. B. Mosola, J. B. Anderson, *Quat. Sci. Rev* **25**, 2177 (2006).
14. B. Kamb, in *The West Antarctic Ice Sheet: Behavior and Environment*, R. B. Alley, R. A. Bindschadler, Eds. (American Geophysical Union, Washington, DC, 2001), pp. 157–199.
15. S. T. Rooney, D. D. Blankenship, R. B. Alley, C. R. Bentley, in *Geological Evolution of Antarctica*, M. R. A. Thomson, J. A. Crame, J. W. Thompson, Eds. (Cambridge Univ. Press, Cambridge, 1991), pp. 261–265.
16. B. R. Parizek, R. B. Alley, *Global Planet. Change* **42**, 265 (2004).
17. Materials and methods are available as supporting material on *Science* Online.
18. A sediment wedge with a rise of 31 m over 8 km and then a fall of 31 m over 3.2 km is typical of the reference experiment; however, because the sediment was added beneath an equilibrated ice shelf and the different models give slightly different equilibrium shelves, the sediment wedges differ somewhat between the models.
19. To good approximation, for a sediment deposit of maximum height h filling a sub–ice-shelf cavity of constant angle θ, relative to the horizontal bed, and with constant angle of repose ϕ, the sediment volume per unit of width is $V = (\cot\theta + \cot\phi)h^2/2$, and the volume increment dV to thicken by dh increases linearly with the wedge thickness as $dV = (\cot\theta + \cot\phi)hdh$.
20. G. K. C. Clarke, *Annu. Rev. Earth Planet. Sci.* **33**, 247 (2005).
21. J. Weertman, *J. Glaciol.* **13**, 3 (1974).
22. Bedrock bumps have the same effect as soft-sediment wedges and are much more likely to be encountered by a retreating grounding line than are sediment wedges. As shown in (*12*), soft-sediment wedges are formed at the grounding line during retreat and may be encountered on readvance, but they are unlikely to survive being overrun by advancing ice, so as to exist beneath grounded ice to influence grounding-line retreat.
23. R. B. Alley *et al.*, *Geomorphology* **75**, 76 (2006).
24. T. K. Dupont, R. B. Alley, *Geophys. Res. Lett.* **33**, L09503 (2006).
25. For sufficiently extensive ice shelves, a 5% decrease in buttressing will require a >5% decrease in the side-drag area.
26. E. Rignot, S. S. Jacobs, *Science* **296**, 2020 (2002).
27. T. A. Scambos, J. A. Bohlander, C. A. Shuman, P. Skvarca, *Geophys. Res. Lett.* **31**, L18402 (2004).
28. J. A. Dowdeswell, A. Elverhoi, *Mar. Geol.* **188**, 3 (2002).
29. J. S. Wellner, D. C. Heroy, J. B. Anderson, *Geomorphology* **75**, 157 (2006).
30. P. Huybrechts, *Quat. Sci. Rev.* **21**, 203 (2002).
31. J. F. Adkins, K. McIntyre, D. R. Schrag, *Science* **298**, 1769 (2002).
32. We thank J. Anderson, H. Horgan, S. Jacobs, D. Voigt, P. Burkett, and other colleagues. Partial funding was provided by NSF through grants (including 0424589, 0440447, 0440899, 0531211, 0447235, and 0539578) and by the Gary Comer Science and Education Foundation

Supporting Online Material
www.sciencemag.org/cgi/content/full/1138396/DC1
Materials and Methods
References and Notes

4 December 2006; accepted 21 February 2007
Published online 1 March 2007;
10.1126/science.1138396
Include this information when citing this paper.

Permissive and Instructive Anterior Patterning Rely on mRNA Localization in the Wasp Embryo

Ava E. Brent, Gozde Yucel, Stephen Small, Claude Desplan*

The long-germ mode of embryogenesis, in which segments arise simultaneously along the anterior-posterior axis, has evolved several times in different lineages of the holometabolous, or fully metamorphosing, insects. *Drosophila*'s long-germ fate map is established largely by the activity of the dipteran-specific Bicoid (Bcd) morphogen gradient, which operates both instructively and permissively to accomplish anterior patterning. By contrast, all nondipteran long-germ insects must achieve anterior patterning independently of *bcd*. We show that *bcd*'s permissive function is mimicked in the wasp by a maternal repression system in which anterior localization of the wasp ortholog of *giant* represses anterior expression of the trunk gap genes so that head and thorax can properly form.

The highly conserved segmented insect body plan is achieved by great flexibility in developmental mechanisms. In the ancestral short-germ mode of embryogenesis, head and thorax arise from the egg's posterior, and abdominal segments emerge progressively from a posterior growth zone. By contrast, in the more derived long-germ mode, all segments form simultaneously in a syncytial environment, with head and thorax at the egg's anterior. Long-germ development has evolved several times in different holometabolous insect lineages (*1*), including the Diptera, of which the most extensively studied member is *Drosophila melanogaster* (*Dm*). A morphogen gradient of Bicoid (Bcd) protein, formed by translation from a maternal, anteriorly localized mRNA source, establishes the *Drosophila* body plan. Embryos derived from *bcd* mutant mothers lack head, thorax, and some abdominal segments (*2*, *3*).

Despite its critical role in patterning the *Drosophila* long-germ embryo, *bcd* is distinctive to the higher Diptera (*4*). Thus, all other insects, including long-germ nondipterans, must employ a *bcd*-independent mechanism to accomplish segmentation. To identify such a mechanism, we investigated anterior patterning in the hymenopteran parasitoid wasp, *Nasonia vitripennis* (*Nv*) (*5*). The embryonic fate map of this independently evolved (*6*) long-germ insect is essentially identical to that of *Drosophila*, except that it is formed in the absence of *bcd*. We previously showed that in the early *Nasonia* embryo, *bcd*'s morphogenetic activity is performed by *orthodenticle1* (*Nv-otd1*), the ortholog of the *Drosophila bcd* target gene, *Dm-otd* (*5*). Although strictly zygotic in *Drosophila*, *Nv-otd1* mRNA is maternally provided and localized to both oocyte poles, resulting in bipolar protein gradients. The anterior *Nv-otd1* gradient regulates expression of zygotic head and thoracic gap genes, including the *Nasonia* orthologs of the *bcd* targets, *giant* (*gt*), and *hunchback* (*hb*) (*5*).

In addition to instructively activating the genes that pattern the head and thorax, *bcd* also functions permissively in *Drosophila* to indirectly repress posteriorly acting genes, such as the trunk gap genes, that would otherwise inhibit anterior development (*7*). We show here that *Nasonia* accomplishes this task by further employing maternal mRNA localization to position a repressor of trunk development at the anterior, thereby allowing formation of the head and thorax.

In the *Drosophila* embryo, the gap gene *Krüppel* (*Dm-Kr*) is expressed in a broad central stripe (Fig. 1A) and is required for formation of thoracic segment 1 (T1) through abdominal segment 5 (A5) (*8*). The positioning of *Kr* and, hence, of the trunk, is established by *bcd* and the terminal system; in embryos derived from *bcd* mutant mothers, the *Dm-Kr* domain broadens and shifts anteriorly (Fig. 1B) (*7*, *9*). *bcd*'s zygotic targets, *Dm-hb* and *Dm-gt*, mediate this regulation; in single *Dm-hb* (*7*, *9*) or *Dm-gt* mutant embryos (Fig. 1C), *Dm-Kr* shows slight anterior expansion (*10*), and in embryos mutant for both, *Dm-Kr*'s anterior shift is comparable to that seen from loss of *bcd* alone (*11*). However,

---

New York University, Department of Biology, Center for Developmental Genetics, 100 Washington Square East, New York, NY 10003, USA.

*To whom correspondence should be addressed. E-mail: cd38@nyu.edu