permit a meaningful test. That leaves observable structure, and here the best indicator would be whether the filaments are tubular or solid in cross-section. Feathers are hollow, tubular structures, and developmental models predict that 'protofeather' filaments should also be hollow[11]. By contrast, collagenous filaments should be essentially solid.

Zheng and colleagues[7] interpret the filaments of *Tianyulong* as being hollow, although it's fair to question their evidence (longitudinal stripes on the filaments). But other attributes of the filaments are also highly suggestive of their being epidermal. For example, the filaments associated with the base of the tail are extremely long, and, given that the tail is already reinforced internally with stiffening rods of ossified tendons, it is possible that these filaments indeed project outside the skin's surface. Even if they can be shown to be definitively epidermal, the ultimate question is whether they are part of the evolutionary lineage of true feathers or an independent evolution of projecting epidermal appendages. Certainly, the finding of very differently structured, projecting, hollow 'bristles' on the tail of another Yixian ornithischian, *Psittacosaurus* (a basal horned dinosaur)[12], raises the possibility that there may be a range of filamentous epidermal structures in dinosaurs, and that not all such structures may be related evolutionarily to feathers[13].

Perhaps the only clear conclusion that can be drawn from the foregoing is that little *Tianyulong* has made an already confusing picture of feather origins even fuzzier. Such an outcome is common in palaeontology. But the prospects of new fossils, new molecular and imaging techniques (such as synchrotron tomography), and even new ideas, offer the hope of bringing the evolutionary picture into sharper focus — and that picture may well end up being of fuzzy dinosaurs. ■

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1. Zhou, Z., Barrett, P. M. & Hilton J. *Nature* **421**, 807–814 (2003).
2. Norell, M. A. *et al. Nature* **416**, 36–37 (2002).
3. Norell, M. A. & Xu, X. *Annu. Rev. Earth Planet. Sci.* **33**, 277–299 (2005).
4. Zhang, F., Zhou, Z. & Dyke, G. *Geol. J.* **41**, 395–404 (2006).
5. Feduccia, A. *et al. J. Morphol.* **266**, 125–166 (2005).
6. Lingham-Soliar, T., Feduccia, A. & Wang, X. *Proc. R. Soc. Lond. B* **274**, 1823–1829 (2007).
7. Zheng, X.-T., You, H.-L., Xu, X. & Dong, Z.-M. *Nature* **458**, 333–336 (2009).
8. Butler, R. J., Upchurch, P. & Norman, D. B. *J. Syst. Palaeontol.* **6**, 1–40 (2008).
9. Witmer, L. M. in *Mesozoic Birds* (eds Chiappe, L. M. & Witmer, L. M.) 3–30 (Univ. California Press, 2002).
10. Chen, P.-J., Dong, Z.-m. & Zhen, S.-n. *Nature* **391**, 147–152 (1998).
11. Prum, R. O. & Brush, A. H. *Q. Rev. Biol.* **77**, 261–295 (2002).
12. Mayr, G. *et al. Naturwissenschaften* **89**, 361–365 (2002).
13. Sawyer, R. H., Washington, L. D., Salvatore, B. A., Glenn, T. C. & Knapp, L. W. *J. Exp. Zool.* **297B**, 27–34 (2003).

GLOBAL CHANGE

West-side story of Antarctic ice

Philippe Huybrechts

During the past five million years, the West Antarctic ice sheet has waxed and waned in size. A two-pronged reconstruction of that history provides clues to the ice sheet's future behaviour.

For human societies, the prospect of sea-level rise is probably the most serious long-term threat from unabated climate warming. Both the Greenland ice sheet and the West Antarctic ice sheet are believed to be vulnerable to warming at the levels projected for the coming centuries. Sustaining those levels for many more centuries or millennia could ultimately cause the demise of both ice sheets — producing a worldwide rise in sea level of about 12 metres compared with today's levels, of which some 5 metres would derive from West Antarctica[1].

The past can be a guide to the future. But the late Quaternary (the past 0.5 million to 1 million years), for which we have the most data, was generally colder than today, and so is not an ideal analogue for the future. The twin papers by Naish *et al.*[2] and Pollard and DeConto[3], published in this issue, now present a step towards filling this gap in data and understanding. In their reconstruction of Antarctica's glacial history, the authors concentrate on the early to middle Pliocene, an interval of time between 5 million and 3 million years ago, when planetary temperatures were more in the range of those projected for the coming centuries.

The suspected vulnerability of the West Antarctic ice sheet stems from its particular setting. It is grounded mostly below sea level and is surrounded by large floating ice shelves (Fig. 1). These floating extensions are in direct contact with the ocean and are widely believed to have a crucial role in keeping the grounded ice sheet in place. At present, Antarctic temperatures are too low to generate significant surface melting during the summer, and this will remain so even with moderate warming. Some combination of sea-level changes and changes in sub-ice-shelf melting must therefore be a key process by which variations in global climate control changes in the West Antarctic ice sheet. A long-standing debate among glaciologists has been the mechanism by which changes to the ice shelf are transmitted inland to grounded ice sheets across their common boundary, the 'grounding line'[4] (Fig. 1), and how effective this mechanism might be.

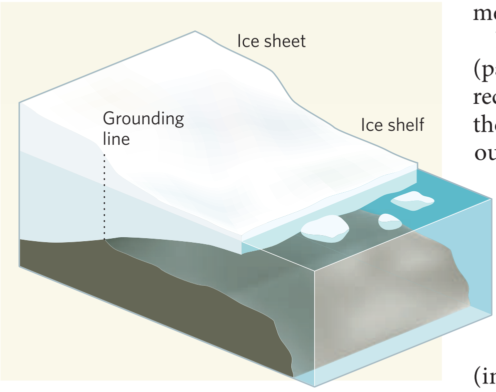

Figure 1 | The West Antarctic ice sheet. This much simplified depiction shows, to the left, the grounded marine ice, which sits upon bedrock or sediment on the sea floor. To the right, separated by the 'grounding line', is the floating ice shelf, which is thought to buttress the grounded ice sheet. The new observational study[2] and modelling work[3] identify a 40,000-year cycle in which the grounding line moves back and forth across the sea floor between glacial and interglacial states, punctuated by periodic ice-sheet collapses with more or less open-ocean conditions during super-interglacials.

Naish and colleagues' observational evidence (page 322)[2] comes from a new sediment core recovered from beneath the Ross Ice Shelf near the current ice-shelf margin. The site turned out to be a strategic location. The range of sediments and rock types and other features seen in the core allowed the authors to distinguish between a cyclical succession of conditions at the drill location: open ocean with little or no summer sea-ice (super-interglacial conditions warmer than those of today); coverage by a floating ice shelf (interglacial conditions much like today's); and overriding by an ice sheet grounded on the sea floor (glacial conditions). Moreover, unlike many other glacial records in which each glaciation has erased the evidence of the previous one, this record stands out in having large sections without such hiatuses because tectonic forces have produced a favourable rate of bedrock sinking.

Dating of undisturbed sections along the core enabled Naish *et al.* to identify 40 sedimentary cycles, each of about 40,000 years' duration, during the Pliocene (up to 1.8 million years ago). These results are in good accordance with the same cyclicity seen in marine-isotope records of global ice volume and mean deep-sea temperatures[5], and are in phase with summer half-year insolation caused by variations of the Earth's tilt at the same periodicity.

The geological sediment data, however, can only provide information on variations of the extent of the grounded ice sheet at one particular location. They provide no indication of ice thickness or, by extension, ice volume, which is where the modelling comes in.

Pollard and DeConto (page 329)[3] used a three-dimensional ice-sheet model to simulate the evolution of the West Antarctic ice sheet in a manner consistent with the geological data. A novel feature of their ice-flow model is the way the different flow regimes of grounded and floating ice are coupled across the grounding line, following the results of recent theoretical work[6]. Although approximations remain, the incorporation of this work in a three-dimensional model is new and is a notable methodological contribution to one of glaciology's grand unsolved problems —the mechanics of how the West Antarctic grounding line migrates over time[4].

The model confirms that the conditions reflected in the sediment core are probably indicative of the evolution of the West Antarctic ice sheet as a whole during the past 5 million years. In addition, the model roughly reproduces much of the inferred ice-sheet variations, ranging from full glacial extents, to intermediate interglacial states similar to those pertaining today, to brief collapses of the entire West Antarctic ice sheet during the warmest super-interglacials. Unlike Antarctic ice-sheet reconstructions produced with broadly similar models, including my own[7,8], Pollard and DeConto find a much more prominent role for sub-ice-shelf melting than for global sea-level variation in driving past migrations of West Antarctic grounding lines.

However, the modelling does not solve every problem. The episodic collapses of the West Antarctic ice sheet during the past 5 million years also happen at times when there is little or no evidence for open-ocean conditions or high sea levels, adding an erratic component to the simulations. Other aspects — such as the timing of grounding-line retreat in the Ross Sea sector since the Last Glacial Maximum, and probably unduly thick ice in this sector both then[9] and today — seem to contradict the observational evidence. This calls for further refinements of processes, such as the sliding of the ice over its bed, that will increase the credibility of the model for supporting predictions on shorter timescales. Other issues concern the rather simple schemes used to prescribe crucial model forcing, such as sub-ice-shelf melting. These would best be addressed by more detailed global-climate and ocean models than are currently possible on these long timescales.

Even so, the modelling by Pollard and DeConto[3] may already be robust enough to attempt to put initial constraints on the amount of nearby ocean warming required to generate enough sub-ice-shelf melting to initiate a significant retreat of the West Antarctic ice sheet. The required ocean warmings, of the order of 5 °C, may well take several centuries to develop. But such an outcome could result from the accumulation of total greenhouse-gas emissions projected for the twenty-first century, if emissions are not greatly reduced[1]. The implied transition time for a total collapse of the West Antarctic ice sheet of one thousand to several thousand years[3] seems rapid by Antarctic standards. But it is nowhere near the century timescales for West Antarctic ice-sheet decay based on simple marine ice-sheet models[10]. ■

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1. Solomon, S. D. *et al.* (eds) *Climate Change 2007: The Physical Science Basis* (Cambridge Univ. Press, 2007).
2. Naish, T. *et al. Nature* **458,** 322–328 (2009).
3. Pollard, D. & DeConto, R. M. *Nature* **458,** 329–332 (2009).
4. Weertman, J. *Nature* **260,** 284–286 (1976).
5. Lisiecki, L. E. & Raymo, M. E. *Paleoceanography* doi:10.1029/2004PA001071 (2005).
6. Schoof, C. *J. Geophys. Res.* doi:10.1029/2006JF000664 (2007).
7. Ritz, C., Rommelaere, V. & Dumas, C. *J. Geophys. Res.* **106,** 31943–31964 (2001).
8. Huybrechts, P. *Quat. Sci. Rev.* **21,** 203–231 (2002).
9. Waddington, E. D. *et al. Geology* **33,** 281–284 (2005).
10. Thomas, R. H. *J. Glaciol.* **24,** 167–177 (1979).

NEUROSCIENCE

Secret of synapse specificity

Scott M. Thompson and Hayley A. Mattison

How does the brain organize all of the information stored in memory? On the basis of a state-of-the-art imaging study of neuronal activity in real time, the answer seems to be, through specificity in space and time.

Memories are encoded by a specific pattern of activity that is unique to the information being processed and stored. Memory formation is almost certainly achieved at the synaptic junctions between neurons through the process of long-term potentiation (LTP), whereby synaptic communication between two simultaneously active neurons becomes stronger[1,2]. One of the many attractions of LTP for explaining the biological basis of memory formation is that it displays remarkable synapse specificity[3,4]: only synapses that are activated become strengthened, and neighbouring synapses located only a micrometre or two away on the same neuron remain unaffected[5]. In an exciting paper on page 299 of this issue, Lee *et al.*[6] study living neurons using advanced fluorescence microscopy to conclusively demonstrate the molecular basis of the synapse specificity of LTP.

A crucial enzyme for triggering LTP is CaMKII. Release of glutamate, a neurotransmitter, from the presynaptic neuron leads to depolarization of the postsynaptic neuron, thus relieving the voltage-dependent block of the NMDA-type glutamate receptors on the postsynaptic neuron, and allowing calcium ions (Ca^{2+}) to enter it. The increased intracellular Ca^{2+} concentration leads to activation of CaMKII, which then phosphorylates itself, thereby remaining active even after the Ca^{2+} concentration has fallen back to normal. Induction of LTP is therefore prevented either by NMDA-receptor antagonists or by CaMKII inhibitors[7].

To image real-time activation of CaMKII in living neurons, Lee *et al.*[6] used the technique of fluorescence resonance energy transfer (FRET)[8]. In FRET, distance-dependent energy transfer from a donor fluorescent molecule (fluorophore) to an acceptor fluorophore nanometres away is measured through changes in fluorescence intensity. Lee *et al.* modified a 'reporter' molecule — the CaMKII-based protein Camuiα[9] — that has a donor fluorophore attached at one end and an acceptor fluorophore at the other. On activation of CaMKII, the donor–acceptor pair moves apart, leading to decreased FRET. The authors further improved Camuiα by using a bright fluorophore, green fluorescent protein (GFP), as the donor and a non-fluorescent acceptor fluorophore[10], a mutated GFP called REACh. Thus, only changes in the emission of GFP need be monitored, allowing emitted photons to be collected in a wider spectral window.

Instead of measuring fluorescence intensity, Lee *et al.* measured the fluorescence lifetime of the donor fluorophore[7]. When CaMKII is inactive, REACh at one end of Camuiα is close enough to quench GFP emission and shorten its fluorescence lifetime. With REACh moving away upon CaMKII activation, however, the fluorescence lifetime of GFP is prolonged (Fig. 1a). That may sound a simple concept, but the lifetime of GFP in the excited state is less than 2 nanoseconds. Extremely brief (<100-femtosecond) bursts of high-energy excitation light must therefore be delivered and high-efficiency detectors of photon emission must be used to measure the time between an excitation pulse and the arrival of an emitted photon.

Finally, to achieve adequate spatial resolution, as well as to detect as many emitted photons as possible, the authors used the technique of two-photon microscopy. This approach was particularly advantageous because of its superior spatial resolution, as the experiments had to be performed in relatively thick slices of