lantic—that is, a sudden warming in the North Atlantic would produce an OCR in the Indian Ocean. This finding (*2*) may solve the OCR problem, but leaves us in limbo regarding the origin of the ACR.

How robust are the findings of Morgan *et al.*? One limitation is that Δage reaches similar values at 15,000 years B.P. as in previous ice cores and that the uncertainties of the synchronization are thus not much reduced (*12*, *13*). The authors therefore present a second chronology for their ice core. With this alternative but less likely chronology, the beginning of ACR occurs at a similar time as in other Antarctic ice cores.

A second problem is not specific to this ice core. Maxima and changes of trends in high-resolution paleoclimatic records may result from natural variations that do not represent large-scale climate signals but are due to local processes. This limitation can only be reduced by additional high-resolution ice cores and a better understanding of local processes.

Further progress will come from new high-resolution Antarctic ice cores (*14*), particularly from locations where a higher fraction of precipitation originates from the Atlantic Ocean. In combination with the vast archive of marine sediment cores, the latter will provide a more spatially complete picture of abrupt climate changes and glacial-interglacial transitions. Recent paleoclimate records from the tropics show remarkable climate fluctuations during deglaciation (*15*), underscoring the necessity to integrate this region more completely into our thinking.

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11. The deglacial OCR can also be detected in the deuterium excess records of other Antarctic ice cores (F. Vimeux, personal communication).
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PERSPECTIVES: GEOLOGY

Genesis of the World's Largest Gold Deposits

Hartwig E. Frimmel

Almost 40% of all gold mined during recorded history has been recovered over the past 120 years from a single ore province: the Witwatersrand Basin in South Africa. Today, the gold-mining industry in the Witwatersrand has passed its maturity, but it is set to remain the world's leading gold producer. Estimated resources in the province still represent ~35% of world gold resources (*1*, *2*).

Despite its enormous economic significance and hundreds of research papers over the past decades, no consensus has been reached on the origin of the gold. A major breakthrough reported by Kirk *et al.* on page 1856 of this issue (*3*) should bring this debate to a close.

Two models have been suggested to explain the formation of the Witwatersrand gold deposits: a sedimentary placer model and a hydrothermal model. According to the former, the gold was introduced into its host rocks by mechanical erosion of gold-bearing hinterland and fluvial transport into a sedimentary basin. Further upgrading of the gold by sedimentary reworking and eolian deflation is indicated by the preferential occurrence of the gold in conglomerate beds above unconformity surfaces (shaped by weathering, erosion, or denudation) and its association with ventifacts (pebbles faceted by the abrasive effects of windblown sand) (*4*). This model finds support from a strong sedimentary control on ore grade, with the Witwatersrand gold being concentrated in the coarsest grained sediments of the succession.

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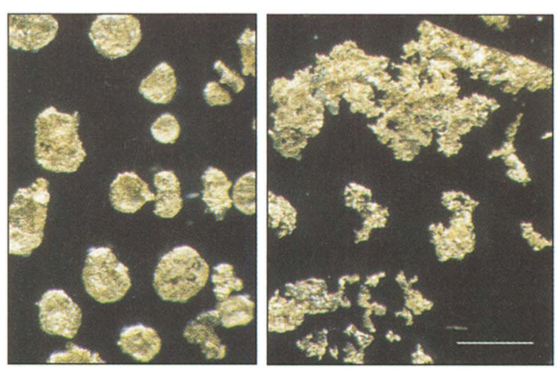

Contrasting morphological types of gold. The gold particles shown here were released by digestion in hydrofluoric acid from a single hand specimen of Witwatersrand ore (9). **(Left)** Rounded, disk-shaped to toroidal, detrital particles. **(Right)** Hydrothermally mobilized, secondary gold. Scale bar, 0.2 mm.

When studied under a microscope, however, most of the gold appears to have crystallized after deposition of the host sediment. Furthermore, the Witwatersrand sediments show signs of having undergone significant metamorphism and hydrothermal alteration. These observations led to the competing hydrothermal models, in which the gold was introduced into the host sediments by hydrothermal or metamorphic fluids (*5*).

A major advance in constraining the age of sedimentation of the gold-bearing strata was recently reported by England *et al.*, who found that most of the gold occurs in sediments deposited between 2890 and 2760 million years ago (*6*). Kirk *et al.* now report Re-Os age data (*3*) that provide the first direct constraint on the age of the gold. The new data are in good agreement with previous attempts to date rounded pyrite and uraninite (*7*, *8*), which are closely associated with the gold. An age of around 3030 million years is now indicated not only for these other heavy minerals but also for the gold.

This is clearly older than the maximum age of sedimentation, and both the gold and the rounded pyrite must therefore have entered the host sediments as detrital particles. The microscopic observation of gold having formed relatively late in the crystallization history of the host rock is then best explained by short-range mobilization and recrystallization of the detrital gold particles during postdepositional deformation and heating of the rocks (*1*). This picture is supported by rare samples in which two types of gold particles are found together on a millimeter scale (see the figure) (*9*): one displaying morphological features that are typical of alluvial, windblown, detrital gold (left panel), and the other occurring as irregular intergrowths of minute, well-shaped hydrothermal precipitates (right panel). The detrital particles are unusual in Witwatersrand ore.

The results of Kirk *et al.* (*3*) confirm that the Witwatersrand gold deposits represent Late Archean placers (ancient detrital sediments transported by a river that contain economic quantities of a valuable material). Furthermore, they provide a possible explanation for the extraordinary size of these deposits. Comparison with the amount of gold extracted from other, younger terrains (*10*) suggests an almost exponential decline in the extraction of gold from the mantle into the crust over geological time.

If this postulated decline in gold extraction into the crust is correct, the uniqueness of the Witwatersrand gold province can be explained by three factors. First, the sediments derive from some of the oldest rocks known on Earth. Second, repeated reworking of sediment led to progressively higher gold grades along degradation and deflation surfaces. Third, the gold-bearing sediments escaped from destruction by later mountain-building processes and/or erosion.

Apart from an obvious application in future exploration strategies for Witwatersrand-type gold deposits elsewhere, the findings of Kirk *et al.* (*3*) also have a bearing on our understanding of the early evolution of Earth's atmosphere. Controversy has existed regarding the oxidation potential of the Archean atmosphere (*11*, *12*). Confirmation of a placer origin not only of the gold but also of the associated pyrite and uraninite implies an overall reducing atmosphere during the Late Archean

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PERSPECTIVES: MEMBRANE FUSION

Caught in the Act

Sol M. Gruner

Membranes divide eukaryotic cells into numerous compartments in which different chemical processes can take place. On page 1877 of this issue, Yang and Huang (*1*) investigate one of the most fundamental processes involving such membranes. They show how membrane fusion intermediates can be stabilized, allowing detailed structural characterization.

The development of the cellular membrane was a defining advance in the evolution of life. Nature's elegant solution to the constraints on living membranes is the lipid bilayer, a structure that is impermeable to most ions and water-soluble molecules, yet flexible, robust, and able to grow and to heal punctures.

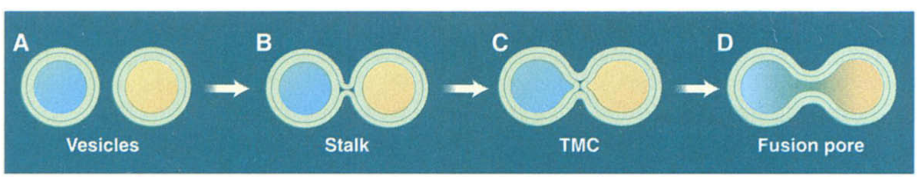
Yet these same properties present problems, because all cells at times need to fuse one membrane compartment with another to mix the contents or deliver new patches of membrane. Scientists have long struggled to understand how bilayers, which seem to be thermodynamically designed to maintain their integrity, can be coerced to fuse and merge with one another.

The primary experimental difficulty in studying this process has been the unstable and highly transient nature of intermediate fusion structures. Yang and Huang (*1*) present an important new experimental tool for studying the fusion process, namely, a stable lattice of lipid fusion structures.

In living systems, fusion is mediated by complex protein machinery. But under appropriate conditions, pure lipid bilayer vesicles can also fuse. It is widely believed that the protein apparatus serves to position the membranes and promote the structural rearrangements that also occur in pure lipid systems, albeit with less control and specificity (*2*). Thus, an understanding of the steps involved in pure lipid bilayer fusion is fundamental to a deeper understanding of the fusion process.

Liquid-crystalline lipid bilayers consist of two opposed monolayer leaflets of highly water-insoluble polar lipids. Within each monolayer, lipid molecules diffuse freely as a two-dimensional fluid. Isolated bilayer vesicles can be brought into close contact—for example, by divalent cations, an electrical pulse, or the addition of hydrophilic polymers. By incorporating fluorescent lipid markers into the bilayers of some vesicles and fluorescent quenchers in others, the mixing of the lipid bilayers upon vesicle fusion can be traced. Similarly, introduction of aqueous fluorescent markers into the aqueous compartment of some vesicles and quenchers into others allows the mixing of the vesicle contents to be monitored.

Such experiments have shown that during fusion, the outer lipid monolayer leaflets exchange molecules before the aqueous compartments. The initial event is the formation of a stalk from locally fused outer leaflets (see panel B in the figure). The radius of the stalk is thought to expand, allowing the inner leaflets to come into contact at the fusion point. This process results in the formation of a transmonolayer contact (panel C) and, upon fusion of the inner monolayers, in a fusion pore (panel D).



Schematic cross section of the fusion of two lipid bilayer vesicles. The vesicle bilayers are schematized as two opposed lipid monolayer leaflets. **(A)** Distinct vesicles. **(B)** The outer leaflets fuse into a connecting stalk. **(C)** The stalk radius widens until the inner leaflets touch in transmonolayer contact (TMC). **(D)** A fusion pore forms.

The challenge has been to understand the energetics of this process. What are the free-energy barriers to fusion of the inner and outer monolayers? And how stable are the various intermediate structures?

Three factors come into play. First, there is a well-understood, steep free-energy cost of exposing lipid hydrocarbon chain seg-

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