News & views

energy regimes than those of aerobic eukaryotes. This kind of metabolism has arisen in various types of anaerobic eukaryote, and is associated with the evolution of mitochondria into organelles called hydrogenosomes⁸. All hydrogenosomes have, to some degree, lost mitochondrial pathways for aerobic respiration, and generate hydrogen rather than carbon dioxide and water as an end product of their energy-generating pathways. Ciliates are exceptionally effective at adapting to oxygen-depleted environments, and mitochondrion-to-hydrogenosome transitions have occurred independently several times in this group of organisms⁹.

Graf and colleagues investigated an anaerobic ciliate belonging to the class Plagiopylea, found in the deepest layers of Lake Zug in Switzerland. This environment lacks oxygen and contains relatively high levels of nitrate. An initial assessment using microscopy revealed that, unusually, these ciliates have a bacterial endosymbiont (belonging to the class Gammaproteobacteria), rather than an archaeal endosymbiont that produces methane, which is the more typical type of endosymbiont present in anaerobic ciliates.

DNA-sequencing data for lake-water samples revealed the presence of genes indicating that the ciliate cells have hydrogenosomes. Moreover, the sequencing data indicate that the bacterial endosymbionts have an electron-transport chain - a collection of protein complexes for respiration that enable energy to be produced by a process called oxidative phosphorylation. Graf et al. propose that the electron acceptor in this chain is nitrate, rather than the oxygen used by aerobic organisms. Consistent with this model, the authors report that rates of denitrification (the microbial process that converts nitrate into nitrogen) were higher in lake-water samples in which ciliates were present than in those from which ciliates had been removed.

The genome of the endosymbiont identified by Graf and colleagues is notably smaller than the genomes of most endosymbionts of microbial eukaryotes, containing a mere 310 protein-encoding genes. Among those, the authors identified a gene that encodes a potential transporter protein for ATP, which they suggest is used to export ATP from the endosymbiont into its host, enabling the ciliate to use the endosymbiont for energy production by 'breathing' nitrate. This finding represents a unique example of an endosymbiont that has contributed the capacity for respiration (albeit using nitrate instead of oxygen as an electron acceptor) to a eukaryote that seemingly retains organelles of mitochondrial descent (hydrogenosomes) - the ancestral versions of which once performed respiratory functions.

Intriguingly, several parallels can be drawn between the cellular partnership discovered by Graf and co-workers and the evolution of mitochondria in eukaryotes. In both cases, respiratory capacity was acquired by an anaerobic host cell through the metabolic integration of a proteobacterial endosymbiont, and mechanisms can be identified for energy exchange between symbiont and host cell. Furthermore, a substantial reduction of the endosymbiont genome is observed, although mitochondrial genomes are typically either much smaller than the endosymbiont genome observed by Graf and colleagues, or have been lost completely (as is the case for several hydrogenosomes¹⁰).

Despite these fascinating similarities, there are also notable differences. Mitochondrial endosymbiosis was a much more ancient event, enlisting an archaeal host cell rather than a modern eukaryotic cell. Mitochondria, even if now reduced from their original form, or even lost from some present-day eukaryotes¹¹, became an integral part of eukaryotic cells. Genes inherited from the original mitochondrial endosymbiont were often retargeted to the nuclear genome, and some of the proteins these genes encoded adopted various functions throughout the cell. A similar level of integration is unlikely for the bacterial endosymbionts of the ciliate investigated.

Nevertheless, it would be interesting to study whether there has been any relocation or repurposing of genes between the host and endosymbiont, and to what extent a typical mitochondrial function, such as ATP

Geophysics

Oceanic fault zones reconstructed

Garrett Ito

Tectonic-plate material is generally thought to be neither created nor destroyed at plate boundaries called oceanic transform faults. An analysis of sea-floor topography suggests that this assumption is incorrect. **See p.402**

At undersea structures called oceanic spreading centres, two tectonic plates split apart, and molten rock from volcanic activity solidifies to produce the crust of the sea floor. These spreading centres are separated into individual segments that are tens to hundreds of kilometres long. At the ends of the segments, shearing (side-by-side sliding) of the two plates occurs along plate boundaries known as oceanic transform faults. Since their discovery in the mid-1960s¹, these faults have been considered as sites where plate material is neither created nor destroyed. But on page 402, Grevemeyer *et al.*² report that this description is too simplistic. They show that, in a several-kilometre-wide region called the transform deformation zone, the crust generated at one spreading segment undergoes episodes of thinning and then regrowth as it drifts towards and past the adjacent segment.

Grevemeyer and colleagues' work was enabled by international collaborations that have supported decades of seagoing expeditions to the world's oceanic spreading centres. The authors analysed sea-floor topography around the intersections between spreading-segment ends and transform faults globally. At these intersections, young crust produced at one spreading segment (the 'proximal' segment) is adjacent to old crust that has been transported

production, has been replaced or retained in the ciliate's hydrogenosomes. Evidence indicating that the ATP transporter identified by Graf and colleagues can export ATP to the ciliate host would help to confirm the proposed symbiotic interaction. Further discovery and exploration of similarly surprising symbiotic interactions in poorly explored parts of the microbial world is certainly an exciting prospect for the future.

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Figure 1 | **Revised understanding of oceanic fault zones.** Oceanic spreading centres are areas at which two oceanic tectonic plates, consisting of a lithosphere (rigid layer) and crust, split apart. At spreading centres, magma rises from a low-viscosity layer called the asthenosphere, and volcanic activity produces the crust of the sea floor. Spreading centres are separated into segments connected by plate boundaries known as oceanic transform faults. In a region called the transform deformation zone (TDZ; blue shaded region), young crust created at the 'proximal' spreading segment is adjacent to old crust that was originally produced at the 'distal' segment. Grevemeyer *et al.*² found that the sea floor rises between the old crust in the TDZ and a connected region known as the fracture zone. They propose that volcanic activity at the proximal segment rapidly reconstructs the TDZ crust adjacent to the fracture zone. They further suggest that J-shaped ridges provide evidence for this process. The authors' modelling also predicts that the TDZ undergoes both shearing (side-by-side sliding; blue arrows) and stretching. The stretching results in cracks and valleys, and explains why the TDZ is deep.

from its place of origin at the other segment (the 'distal' segment).

The authors found that the sea floor of the old crust in this transform deformation zone (TDZ) is consistently deeper than the sea floor in the fracture zone (FZ) – a scar of fractured crust where this old crust has already drifted past the proximal segment, and shearing has ceased (Fig. 1). This rapid shoaling (rise in sea-floor elevation) is opposite to the gradual sinking expected, considering that, in migrating from the TDZ to the FZ, the crust continues to age, and should therefore cool and become denser.

Grevemeyer *et al.* then examined systems of spreading segments that represent the global range of sea-floor-spreading rates. They discovered that the depth of the TDZ tends to be maximal when sea-floor spreading is ultraslow³ (slower than 20 millimetres per year) or slow ($20-55 \text{ mm yr}^{-1}$), and minimal when spreading is relatively fast ($55-140 \text{ mm yr}^{-1}$). To explore the physical causes of this relationship, the authors produced computer models that simulate deformation in the volume of crust and mantle below a transform fault joining two spreading segments.

As expected, Grevemeyer and colleagues found that the geometry of the plate boundary leads to shearing in the TDZ. However, by accurately simulating deformation of the brittle lithosphere (the crust and uppermost mantle)⁴, the authors determined that the TDZ also undergoes horizontal stretching. This stretching thins the lithosphere, causing the TDZ to deepen. The computer models predict that the amount of stretching and deepening increases with increasing difference in the crustal age across the TDZ. This difference increases with decreasing spreading rate because, at lower rates, the crust from the distal segment takes longer to reach the proximal segment. Therefore, the authors' models explain the newly discovered global relationship between spreading rate and TDZ depth.

Grevemeyer *et al.* attribute the rapid shoaling between the TDZ and the FZ to magma produced beneath the spreading centre that periodically overshoots the proximal-segment end (for example, in magma-filled fractures) and reconstructs the TDZ crust. The evidence for this overshooting is seen in a series of J-shaped ridges that run parallel to the proximal segment and extend across the TDZ-FZ intersection, hooking inwards towards the TDZ (Fig. 1). Further signs of such volcanic reconstruction include circular volcanic domes and other hilly topographic features.

Such J-shaped ridges have been noted in studies of systems in which the spreading rate is intermediate⁵ or fast⁶. However, Grevemeyer *et al.* document the prevalence of these features at all spreading rates, and assert that the ridges have a widespread role in this new concept of transform-fault evolution. Moreover, the authors make the striking observation that the amount of shoaling between the TDZ and the FZ seems to be independent of the spreading rate. This finding suggests that the degree of volcanic reconstruction is as high at cool, magma-starved slow-spreading systems as it is at hot, magma-rich fast-spreading systems.

Grevemeyer and colleagues' discoveries and interpretations are compelling, but also demand further investigation. For example, future studies should aim to reconcile the predicted horizontal stretching of the TDZ with the fact that earthquakes along oceanic transform faults are mainly associated with shearing⁷ rather than stretching⁸. Moreover, further modelling work should examine whether the results of the authors' model persist under more-realistic conditions than those considered in their paper. For instance, such work could consider topography supported by dynamic stresses9, surface faults and stateof-the-art deformation laws derived from rock physics.

Regarding volcanic reconstruction, seafloor seismic studies are needed to test the hypothesized crustal thickening and to reconcile discrepancies between the evidence presented by Grevemeyer and colleagues and that reported in a previous study¹⁰ especially, evidence from gravity measurements that suggests crustal thickening does not occur at slow-spreading systems. Finally, it is unclear whether the magma that forms the J-shaped ridges originates beneath the spreading centre and propagates laterally, as proposed, or is generated locally below the TDZ-FZ intersection, rises mostly vertically and is guided into the J shape by lithospheric stresses. Resolving this issue will require some combination of modelling, detailed sea-floor observations, and sampling and chemical analysis of the lava rock of the ridges. Such work is also crucial for an improved understanding of the physics of magma generation and transport near all types of plate boundary.

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