Leaving negative ancestors behind

Bacteria with a single cell membrane have evolved from ancestors with two membranes on multiple occasions within the Firmicutes phylum.

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For more than a century bacteriologists have used the Gram stain reaction to classify bacteria. The Gram stain is a violet-colored dye that is retained by Gram-positive bacteria but not by Gram-negative bacteria. These different reactions to the stain reflect fundamental differences in the cell envelopes of these bacteria: Gram-positive bacteria usually have a single cell membrane that is encased by a thick wall made of a polymer called peptidoglycan, whereas Gram-negative bacteria tend to have two membranes with a thin wall of peptidoglycan sandwiched between them.

The tree of life contains about 30 bacterial phyla, but only three of them contain bacteria that are surrounded by a single cell membrane, which are also known as “monoderms”. The remaining phyla contain bacteria with two cell membranes, and most of these “diderms” have large molecules called lipopolysaccharides (LPS) in their outer membranes. However, at least two phyla comprise diderms that do not have LPS.

The evolutionary relationships between monoderms and diderms have remained uncertain for many years. It is generally thought that the monodermic cell plan evolved from the more complex didermic cell plan in a single simplification event (see, for example, Cavalier-Smith, 2006). However, it is possible that diderms could have evolved from monoderms (Dawes, 1981; Tocheva, 2011). Now, in eLife, Simonetta Gribaldo of the Institut Pasteur and co-workers – including Luisa Antunes and Daniel Poppleton as joint first authors – report that monodermic bacteria evolved from ancestral didermic bacteria not once but multiple times by losing the outer membrane from their cell envelopes (Antunes et al., 2016).

Comparative analyses of the genomes of Negativicutes and Halanaerobiales also allowed Antunes et al. to make inferences about the nature and evolution of their didermic envelopes. Notably, and unusually, most of the genes
required for the biogenesis of the outer membrane clustered in a large genomic region in both groups. Moreover, these two groups have envelope appendages (such as flagella and pili) that resemble the envelope appendages of other diderms (in other phyla) more than they resemble those of their close monodermic relatives. Finally, didermic firmicutes appear to retain ancestral systems for the biogenesis of their outer membranes.

The root of the bacterial tree of life remains a mystery and we do not know whether the last common ancestor of all bacteria was a monoderm or a diderm, and whether it produced endospores or not. It is reasonable to assume that the classical diderms that contain LPS have a single origin (Sutcliffe, 2010; Tocheva et al., 2016; Sutcliffe and Dover, 2016), and that they plausibly evolved via an endospore released by an ancestral monoderm (Dawes, 1981; Vollmer, 2012; Tocheva et al., 2011). And now the work of Antunes et al. suggests that most Firmicutes lineages became secondarily monodermic on multiple occasions. Is the same true for the Actinobacteria and the Chloroflexi, the other two phyla that contain monodermes? It is also noteworthy that the three monodermic phyla tend to cluster in many analyses, and are relatively close to the presumed root of the bacterial tree of life (Raymann et al., 2015; Hug et al., 2016), although resolution remains poor at the deepest phylogenetic levels. A more robust phylogenetic framework for bacteria is needed to make sense of these observations.

To better understand the large-scale evolutionary history of bacteria, we need to answer why, how and when the major structural differences among the prokaryotes (bacteria and archaea) came to be. Antunes et al. have provided some answers to the last question (and also shown that a given major structural change can happen more than once), and planted the seeds to answer the first two questions with regard to the evolution of monodermic bacteria. Future biochemical, ultrastructural and genomic characterization of novel prokaryotic lineages, such as the CPR taxa (short for candidate phyla radiation taxa; Hug et al., 2016), will provide more raw material to reconstruct the phenotypic evolution of prokaryotes. The syntheses of these data, together with a robust phylogenetic tree of the prokaryotes, will no doubt provide new insights into the major changes in cell evolution and help to clarify the nature of the last common ancestor of bacteria.
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