

homologues (one-half of a chromosome pair) into the daughter cells. This process creates unique and genetically diverse individuals, some of which will have genotypes that are well suited for survival under changing environmental pressures. Inbreeding can unmask deleterious mutations when these are passed on in the germ line of both parents. Indeed, each human contains hundreds of seriously damaged genes, but these 'balanced lethal mutations' are compensated for by the presence of a fully functional copy of the gene from one parent. Outbreeding and meiosis therefore ensure evolutionary fitness and minimize the accumulation of harmful mutations.

But some organisms seem to be non-meiotic, so how do they cope? They have evolved other strategies to create genetic diversity, and *C. albicans* is a good example. Its genome contains most or all of the genes that would be required for sexual reproduction by meiosis, but meiosis has never been observed in this species. It has even been suggested that meiosis may be impossible in *C. albicans*, because of balanced lethal mutations scattered throughout the genome of diploid strains that would result in non-viable haploid progeny.

Some genetic variation will be introduced by recombination during mitosis (the replication of diploid cells) and by homozygosis (a process in which one of the two strands of DNA in the chromosomes becomes replicated at the expense of the other). But, in the absence of full meiosis, *C. albicans* uses other reproductive strategies that generate variability. The fungus can mate efficiently as long as it is in a mating-competent cell form called the opaque phase³ — in this phase, diploid cells fuse together to form tetraploid progeny^{4,5}. During this 'parasexual cycle', the tetraploid progeny gradually shed chromosomes to regenerate the diploid state⁶. This 'concerted chromosome loss' seems to be non-meiotic in that it does not result in the chromosome-segregation pattern that would be predicted from meiosis. *C. albicans* can also specifically duplicate some chromosomes to generate aneuploid strains (which have an abnormal number of chromosomes), a process that occurs under the selective pressure exerted by antibiotics⁷. Finally, same-sex mating of diploids (homothallism) has also been reported⁸.

Hickman and colleagues' results add to the repertoire of genetic-reassortment mechanisms for this apparently asexual organism. During a screen of *C. albicans* strains to find those that harbour genetically identical chromosome pairs (homozygous strains), the authors discovered rare strains that had lost a single copy of each of the eight chromosomes and become haploid, apparently by a concerted-chromosome-loss mechanism (Fig. 1). Although previous work had demonstrated that individual chromosomes could be lost⁶, this study establishes that true haploids

of *C. albicans* can be generated by this process, and that these are viable.

The authors found that these haploid strains arose both in laboratory cultures and during infections of mice. The haploids were fully competent to grow as yeasts or to form hyphal filaments (which can invade human tissues) as well as opaque-phase cells that could mate with cells of the opposite mating type. The haploids could also mate with themselves or duplicate single chromosomes to form spontaneous 'auto-diploids' (Fig. 1). The haploid and auto-diploid strains were, however, slower growing and less virulent than their parental heterozygous diploids, and were outcompeted by heterozygous diploid strains in mouse infection models. This accounts for the rareness of these haploid strains and why they have not previously been detected.

Interestingly, Hickman and colleagues also found that the two homologues of each chromosome were not equally likely to be lost during haploid formation. For five of the chromosome pairs, only one homologue was lost, suggesting that this process weeds out chromosomes that harbour lethal gene variants. The possibility therefore emerges that forming mating-competent haploid cells helps to eliminate lethal mutations from the population. The reduced fitness of haploid strains and homozygous auto-diploids relative to the parental diploids is presumably a result of uncovering harmful, but not lethal, mutations. This view is supported by the authors' observation that crossing non-identical haploid strains generated partially heterozygous strains with

notably increased fitness. Thus, this mechanism achieves many of the attributes of sexual reproduction, but without meiosis.

The revelation of this rare ability of *C. albicans* to generate haploid strains adds to the array of alternative mechanisms for genetic recombination used by this fungus in the apparent absence of meiosis. The identification of these strains also opens the way for the development of experimental technologies and resources that are difficult to construct in diploids. Libraries of fungal mutants can now be produced on a haploid background, and genetic crosses can be performed to combine genotypes of interest. *C. albicans* causes around 400,000 potentially lethal infections each year¹, and a better understanding of the pathogen's biology may help us to tackle these. ■

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ASTROPHYSICS

Going supernova

When massive stars die as supernovae, these explosions can be seen out to the 'edge of the Universe'. But the stars' nature is often unclear. New observations provide insight into the life of one such star before it exploded. [SEE LETTER P.65](#)

ALEXANDER HEGER

Massive stars die violently. Born with masses greater than about ten times that of the Sun, they end their lives as supernovae or powerful γ -ray bursts. But how do they look just before they die? On page 65 of this issue, Ofek *et al.*¹ report observations of an outburst from a massive star just 40 days before it exploded as a supernova. Rare observations such as these offer a means to probe the brief terminal phases of massive stars that are not otherwise easily accessible.

Before 1987, astronomers thought that massive stars evolve to become red supergiant stars and then explode. But then supernova SN 1987A, the closest supernova to be observed since the early seventeenth century,

was detected in the Small Magellanic Cloud², a nearby dwarf galaxy. Because of its proximity to Earth, researchers were able to look at archival data and identify what had been at the location of the supernova. It came as a surprise that the supernova's progenitor star³ was actually a blue, rather than a red, supergiant. But SN 1987A was an unusual case because of its proximity. Nowadays, large observational programmes are in place to study supernovae and their progenitors in nearby galaxies on a regular basis. Some of these programmes have found⁴, for example, that the progenitors are typically less massive than expected. But much remains unknown about their exact nature, particularly just before they explode.

Stars are powered by nuclear-fusion processes in their interior, where light elements

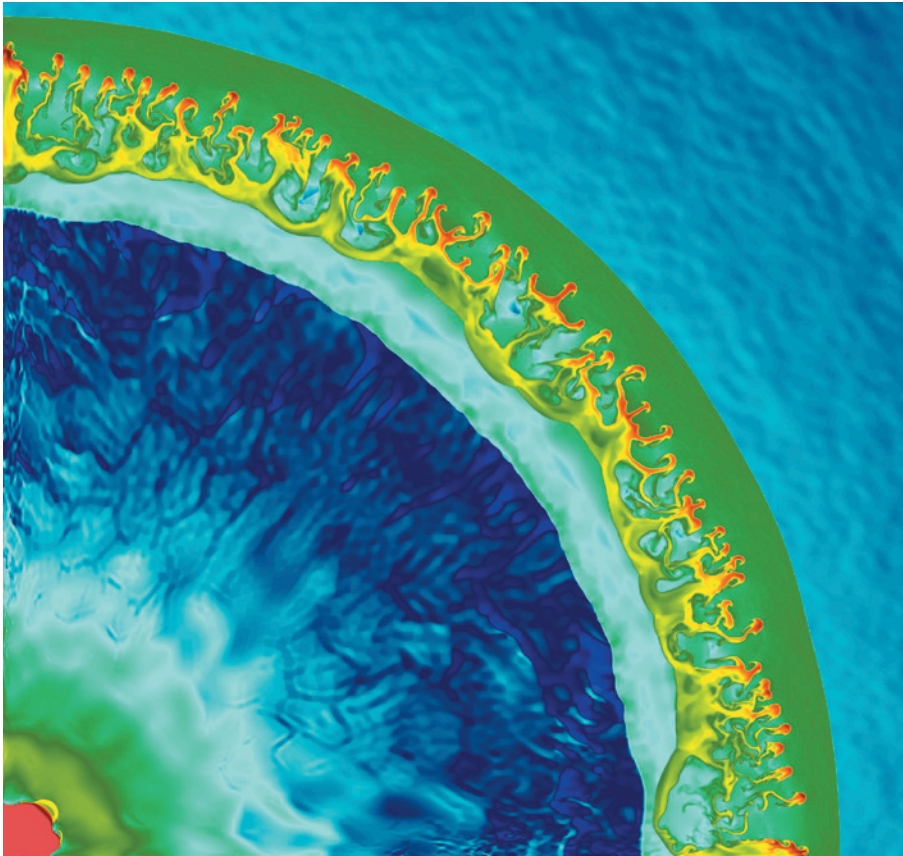


Figure 1 | Shell collision. The image shows a simulation of a collision between two shells of matter ejected by a massive star in two subsequent pulsational pair-instability supernova eruptions¹¹, only years apart, just before the star dies. Displayed is a slice through the upper-right corner of the event. The radius of the shell that contains collision fragments (red knots) is about 500 times the Earth–Sun distance. The colour coding represents gas density ranging from 10^{-11} to 10^{-16} grams per cubic centimetre, with red indicating the highest density and dark blue the lowest. (Image courtesy of Ke-Jung Chen, School of Physics and Astronomy, Univ. Minnesota.)

are forged into increasingly heavier ones⁵. They spend most of their time fusing hydrogen into helium. Then, all but the least-massive stars fuse helium into carbon and oxygen, a stage that takes most of their remaining lifetime. For stars born with more than about six to seven times the Sun's mass, fusion continues and carbon is converted into oxygen, neon and magnesium. For stars born with less than about eight to ten times the Sun's mass, fusion at the star's centre stops, and eventually the star becomes a white dwarf. More-massive stars continue the fusion process in their core at increasingly higher temperature and density, producing silicon and sulphur and finally elements near iron in the periodic table. These elements have the most tightly bound nuclei, and no energy can be gained from fusing them. This 'ash' accumulates in the star's centre and the star ultimately collapses owing to the pull of gravity. In most cases, the star explodes as a supernova, leaving behind a neutron star or a black hole⁶. But some of the most massive stars may contract rapidly soon after using up their carbon, burning much of their remaining fuel in just seconds. This could lead to complete disruption of the star in a powerful

explosion that leaves no remnant⁷, or in a series of supernova-like eruptions of shells of matter, known as pulsational pair-instability supernovae, shortly before the star dies. The collision of subsequent shells of ejecta can trigger some of the brightest observational displays in nature⁸ (Fig. 1).

The advanced burning stages of massive stars are peculiar. The star loses most of its energy, not in the form of observable light from its surface, but rather through neutrinos that escape from the hot centre and cool the star. As a result, these late stages proceed quickly relative to the star's total lifetime of a few million years: the fusion of carbon lasts hundreds of years, and silicon fusion may occur in just a week. Until recently, no sign of these advanced burning stages was expected to become visible at the star's surface, and so it was impossible to tell at which point a star was in its late evolutionary phase, or how soon it would go supernova. Measuring the neutrinos released would offer a window into this phase, but this is a difficult, if not currently impossible, task, even for the closest massive stars, such as Betelgeuse⁹.

In their study, Ofek and colleagues observed

an outburst of about 0.01 solar masses of material from a massive star just roughly one month before it exploded. They suggest that the progenitor star was a fairly massive object, about 50 solar masses. On the basis of statistical considerations, they argue that this eruption is causally related to the ensuing supernova explosion. If confirmed, this system would represent one of the few cases in which additional information has been obtained about the late life of a fairly massive progenitor star — other than that gained from analysing the composition of ejected material or from the supernova itself. Stars with initial masses larger than 20–25 solar masses are found to undergo eruptions. One extreme example of such an eruption is that experienced by the nearby, very massive star Eta Carinae, which may have shed 20 of its initial 150 solar masses in just a few years¹⁰. For most eruptions in massive stars, however, we know little about when they occur and what drives them.

Ofek *et al.* assessed their data within the framework of various theoretical models for such eruptions. They concluded that the timing and nature of the ejecta are best described by a model¹¹ based on hydrodynamic instabilities in the last stages of fusion. But more theoretical work is needed to model these eruptions and to understand the underlying mechanisms. It will also be interesting to investigate how these outbursts relate to other eruptive events observed in similarly massive stars but which are not connected to the final fusion stages. How can the different types of event be teased apart before the supernova is observed? Nevertheless, Ofek and colleagues' observations may change our understanding of the final evolutionary stages of the most massive stars, just as supernova SN 1987A did for their less-massive cousins. ■

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