these effects almost cancel, and we may not need to revise our value of $H_0$ after all.

My assessment of the various systematic effects is a personal one, and not everyone agrees with it. For instance, according to a recent review article $^{19}$ the distance to the LMC is 55 kpc, which is even larger than the value adopted by the HST Key Project. Clearly, systematic effects and personal judgements dominate published values of $H_0$. This may get better following the release of 340,000 photometric measurements of 1,300 LMC Cepheids by the OGLE (Optical Gravitational Lensing Experiment) team $^{17}$, which are available for everyone to analyse using their favoured methodology.

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**Biophysics**

**Fungus punches its way in**

Nicholas P. Money

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The development of a specialized fungal cell known as the appressorium is a wondrous story. This microscopic structure inflates on the surface of a grass leaf, then generates enough force to push through the fatty plant cuticle and glassy epidermal cell wall to tap the juices within. Clemens Bechinger and colleagues have made a breakthrough in understanding how this infection platform works, by using an optical method to measure the forces produced by a single appressorium. This work, reported in Science $^2$, verifies earlier predictions about the magnitude of the invasive force, pushing us closer to a comprehensive picture of the penetration mechanism.

Our understanding of appressorial development draws on experiments using two of the most important cereal pathogens — *Magnaporthe grisea* (the rice blast fungus) and *Colletotrichum graminicola*. Infection is initiated when a fungal spore lands, and germinates, on the surface of the host. The appressorium develops as a swelling at the tip of the developing fungal filament (hypha), and the structure becomes bonded to the host by a strong glue $^{2,3}$. Maturation involves the deposition of melanin within the appressorial wall, and, as the appressorium blackens, accumulation of osmolytes such as glycerol in the cytoplasm $^4$. These osmolytes draw water into the appressorium, generating extraordinary levels of intracellular turgor pressure $^5$. Following this increase in turgor, a thin penetration hypha extends from the base of the appressorium and perforates the host surface.

Although we know much about how appressoria function, the absence of methods to measure the invasive forces that they exert has long posed a problem for those studying mechanical interactions between pathogenic fungi and their hosts. Bechinger and colleagues’ solution is both ingenious and elegant.

Appressoria will form not only on plant leaves, but also on a variety of hydrophobic surfaces. Some years ago, we reported $^6$ that appressoria can penetrate Mylar and Kevlar (poly(ethylene terephthalate) and poly(phenylene terephthalamide, respectively), sparing visions of bulletproof vests destroyed by airborne moulds. In Bechinger and colleagues’ experiments, appressoria of *C. graminicola* formed on an aluminum surface that was part of a metal sandwich (called a waveguide) enclosing a 1-μm-thick layer of the viscous silicone compound used in breast implants. As the fungus began its futile attempt at penetration, each appressorium deformed the aluminum and underlying gel.

The depth of these indentations (which is proportional to the applied force) was measured by illuminating the sandwich with a laser. Laser light is propagated through the waveguide, and it reflects at the upper interface between the silicone and the aluminum. So, the angle of incidence at this interface depends on any deformation of the otherwise flat aluminum. By collecting data on the intensity of the reflected light with a CCD camera, the authors built a three-dimensional image of the waveguide’s surface as the laser scanned the interface. This provided them with vertical spatial resolution in the nanometre range. To determine the forces exerted by appressoria from these spatial measurements, the authors calibrated the waveguide by probing with a glass capillary of known spring constant using forces up to 35 μN.

The appressorium derives its invasive force from its turgor pressure. This has been

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measured by incubating appressoria in solutions of increasing osmolality until they deflate to atmospheric pressure, and also by measuring the melting point of intracellular ice\textsuperscript{5,6}. Estimates have exceeded 8 MPa or 81 atmospheres — the highest turgor pressures on record. The actual force does not depend entirely on turgor pressure, though. It is affected by both the size of the penetration hypha and the degree to which its cell wall yields: the looser the wall, the more of the force within the appressorium will be exerted on the substrate underneath\textsuperscript{7}. According to Bechinger and colleagues, appressoria of \emph{C. graminicola} exert an average force of 17 \(\mu\text{N}\). This figure is remarkably close to estimates published for \emph{M. grisea} (up to 8 \(\mu\text{N}\)) based on the pressure data\textsuperscript{8}.

Some details of the mechanical interaction between the appressorium and resistant surfaces remain in question. Measurements of impressions made by a metal probe at various loads (the Vicker's indentation technique) have shown\textsuperscript{9} that appressoria can penetrate Mylar films with hardness values exceeding 200 MPa (or \(2 \times 10^{7}\) \(\text{N m}^{-2}\)). To relate this measurement to the process of penetration, it needs to be scaled down to the size of a penetration hypha (about 1 \(\mu\text{m}\)). The prediction from these measurements is that a cell of this size must exert 200 \(\mu\text{N}\) to penetrate the Mylar film. Yet Bechinger and colleagues' waveguide data indicate that the force is ten-fold lower.

How can we explain this paradox? Perhaps Vicker's method overestimates the force necessary to penetrate Mylar on a microscopic scale. Or maybe the fungus has some mechanism for softening this compound, although no enzyme has yet been identified that can degrade it. Moreover, although it can be pierced by appressoria, Mylar has proved incredibly resistant to microbial degradation in long-term trials. But even if appressoria do not operate by mechanics alone, 17 \(\mu\text{N}\) is a tremendous force for a cell — if a force of 17 \(\mu\text{N} \text{ mm}^{-2}\) were exerted over the palm of one hand, a human could lift an 8,000-kg school bus. Bechinger and colleagues' report has, then, added to a picture of awesome microbial power that was already quite familiar to fungal biologists.

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**High-temperature superconductivity**

**Electrons pair themselves**

Joe Orenstein

Soon the discovery of high-temperature superconductivity in copper-oxide materials will belong to a previous millennium. In the early days an explanation of this phenomenon was expected well before the next epoch, but the 1990s saw the mystery settle like an indigestible dinner at a roadside restaurant. Some new insights, such as the paper from Carbotte et al.\textsuperscript{1} on page 354 of this issue, may offer a dose of much needed relief.

Bardeen, Cooper and Schrieffer (BCS) explained superconductivity seen in conventional metals when cooled below the transition temperature, \(T_c\), back in 1957. The essential ingredient of their theory is the interaction between freely moving electrons and the lattice of ions that form the structural basis of the solid. This interaction leads to a net attraction and pairing of electrons. Although each electron is a type of particle known as a fermion, a pair of electrons becomes a composite boson (a particle that obeys completely different quantum statistics). Superconductivity can be viewed as a condensed phase analogous to a Bose–Einstein condensate of atoms.

Immediately after the discovery of high-\(T_c\) superconductivity, it was expected that a reasonable theory for the copper oxides might come from 'BCS on steroids' — a beefed-up version of the same electron-lattice mechanism. This idea received support from measurements of the magnetic-flux quantum in copper oxides, which showed the superconducting condensate to be composed of electron pairs\textsuperscript{2}. Later advances in materials fabrication led to the dramatic discovery that the electron pairs have \(d\)-wave orbital symmetry rather than \(s\)-wave, an observation that does not fit into the electron-lattice theory\textsuperscript{3,4}.

With the lattice seemingly out of the picture, the search began for another type of 'glue' to bond electrons into pairs. At present no external bonding agent has been found. Without such an agent we must conclude that electrons can pair and condense despite the repulsion of their negative charges, and that they do so at spectacularly high temperatures. Can electrons act as both gluer and gluee?

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**Figure 1** Absorption of a photon by a superconductor. Shaded circles illustrate the region of momentum space occupied by electrons in their superconducting ground state. Photon absorption promotes an electron to an unoccupied state, leaving a hole behind. Because the photon has nearly zero momentum, photogeneration of the electron-hole pair alone is forbidden by momentum conservation. In BCS superconductors a phonon with momentum opposite to that of the electron-hole pair is generated as well. Absorption occurs when the photon energy equals the sum of the phonon energy \(\hbar \omega\) and the gap energy \(E_g\). In high-\(T_c\) superconductors the coupling of electrons to each other may play a more important role than the electron-lattice coupling that drives superconductivity in BCS superconductors. In this case, photon absorption generates an exotic final state comprising two electron-hole pairs.