were attracted to ovules and entered the micropyle, but failed to burst and release sperm, continuing to grow instead. This phenotype suggested failed communication between the pollen tube and the embryo sac, but it was not known whether *feronia* and *sirène* affected the same or different components in this dialog. Escobar-Restrepo *et al*. now show that both mutants have lesions in the same gene and that the gene encodes an enzyme that phosphorylates proteins on serine and threonine residues. The enzyme, FERONIA, belongs to the previously uncharacterized CrRLK1L-1 group of receptor-like kinases (*4*), of which there are 15 members in *A. thaliana*. The authors determined that FERONIA is located in the plasma membrane of the synergid cells.

Because the pollen tube overgrowth phenotype resembled that seen after interspecies crosses in *Rhododendron*, Escobar-Restrepo *et al.* tested whether crosses with *A. thaliana* relatives would yield similar phenotypes and thereby implicate FERONIA in interspecies barriers. Indeed, crosses of *A. thaliana* females with *Cardamine flexuosa* pollen or with pollen of a more closely related species, *Arabidopsis lyrata*, yielded a pollen tube overgrowth phenotype. Recent studies suggest that synergid cells secrete a pollen tube attractant (*5*–*7*). In addition, an ovule already targeted by a pollen tube may produce a repellent to ward off additional pollen tubes (*7*). Moreover, these attractants and repellents exhibit some degree of species specificity (*7*, *8*). In both *sirène* and *feronia* mutant plants, some ovules attracted more than one pollen tube (*2*, *3*), perhaps because the attractant persists when the first pollen tube does not burst.

Proteins involved in sexual recognition can show amino acid diversification in regions that interact with a protein from the other sex (*9*) as the proteins evolve to match each other; that is, genes with increased rates of evolution increase the frequency with which incompatibilities evolve between closely related species. Among plants related to *A. thaliana*, the extracellular domain of FERONIA has more nonsynonymous nucleotide changes than the highly conserved kinase domain. This suggests that the presumed ligand-binding region was subject to positive selection and that coevolution between FERONIA and an equivalently diverging ligand could contribute to reproductive isolation.

Escobar-Restrepo *et al.* propose a signaling pathway wherein ligand from the pollen tube interacts with FERONIA, causing the synergid cell to send another signal back to the pollen tube to stop growing and burst (see the figure). Much more information is needed to test this intriguing model. The immediate challenge is to identify the FERONIA ligand. There is no way to guess a priori what it might be; even within the LRR (leucine-rich repeat) receptor kinase group—the best-studied such group in plants—the known ligands are diverse (*10*). Potential ligand-receptor pairs might be identified through screens of mutant plants for similar phenotypes (*11*) such as pollen tube overgrowth. Yeast two-hybrid screens (*12*) are another option, in which the extracellular domain of FERONIA can be used as bait for complementary DNA libraries prepared from germinated pollen tubes.

It will also be important to determine whether disruptions of *FERONIA* homologs in other species give similar phenotypes; if so, the pollen overgrowth phenotype may occur with interspecies crosses in other plant families. It is intriguing that in the cross with *A. lyrata*, 50% of the pollinated *A. thaliana* ovules showed the pollen overgrowth phenotype, whereas the other 50% showed normal fertilization (*1*). Indeed, interspecies crosses with *A. lyrata* are possible (*13*). Escobar-Restrepo *et al.* suggest that there might be different isoforms of the ligand in *A. lyrata*, with one allelic variant that recognizes the *A. thaliana* version of FERONIA.

FERONIA and its upstream and downstream signaling partners may be the key to successful sperm discharge. If so, then manipulating the components of this pathway might facilitate more promiscuous hybridizations than occur in nature.

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ASTRONOMY

Seeing Through Dark Matter

Stacy McGaugh

Dark matter was proposed to explain galaxy dynamics. A modification of Newton's law of gravitational force may offer a better explanation.

The universe appears to be dominated by invisible components that astronomers call dark matter and dark energy. The astronomical evidence implicating dark matter has been apparent for a generation (*1*): The rotational speeds of objects in extragalactic systems exceed what can be explained by the visible mass of stars and gas. This discrepancy has led to the inference that there is more mass than meets the eye. However, this inference requires that Newton's law of gravitational force be extrapolated well beyond where it was established. In addition, laboratory searches for dark matter have yet to bear fruit. This lack of corroboration, combined with the increasing complexity and "preposterous" nature of a once simple and elegant cosmology, leads one to wonder if perhaps instead gravity is to blame.

Simply changing the force law on some large length scale does not work (*2*). One idea that has proven surprisingly resilient is the modified Newtonian dynamics (MOND) hypothesized by Milgrom (*3*) in 1983. Rather than change the force law at some large length scale, MOND subtly alters it at a tiny acceleration scale, around 10^{-10} m s^{-2}. In systems with gravitational accelerations above this scale (e.g., Earth, the solar system), everything behaves in a Newtonian sense. It is only when accelerations become tiny, as in the outskirts of galaxies, that the modification becomes apparent.

MOND has successfully described the rotation curves of spiral galaxies (see the figure) (*4*). In case after case, MOND correctly maps the observed mass to the observed dynamics. Why would such a direct mapping exist between visible and total mass if in fact dark matter dominates? Moreover, MOND's explicit predictions for low surface brightness galaxies have been realized (*5*). In contrast, the dark matter paradigm makes less precise predictions (*6*) for rotation curves that persistently disagree with the data (*7*).

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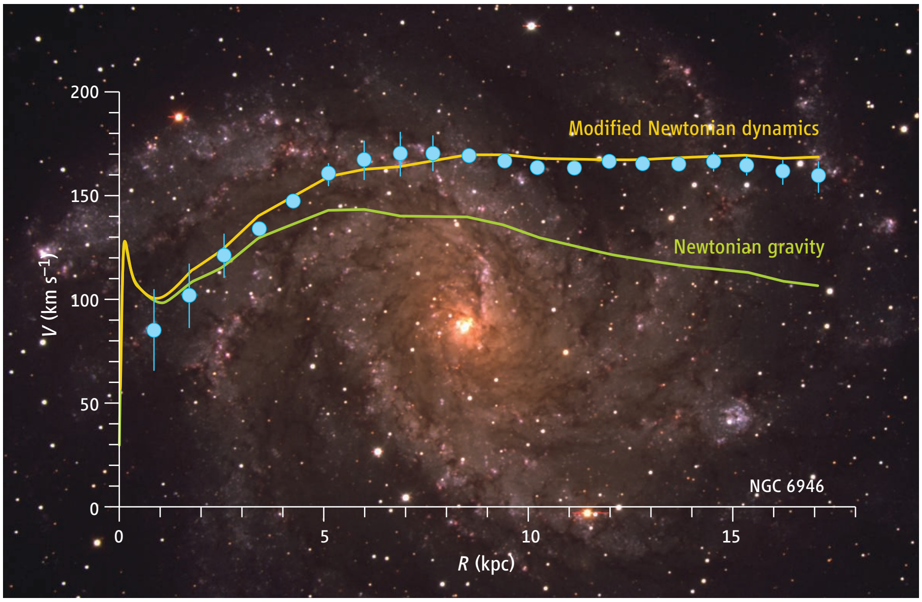
One problem is that researchers have found it difficult to create a version of MOND that satisfies the well-established tests of Einstein's general theory of relativity. This hurdle has now been overcome by Bekenstein (*8*). Testing Bekenstein's approach is in the early stages, but initial results look promising (*9*).

Despite the observational and theoretical successes, the picture for MOND is not all rosy. Many observations purport to falsify MOND, although often the evidence is less compelling than might be hoped. Perhaps the most serious observational challenge is from rich clusters of galaxies. These systems exhibit clear mass discrepancies that MOND fails to completely rectify (*10*). Even after application of the MOND formula, one still infers that there is as much unseen mass in these clusters as can be seen in stars and gas. Consequently, MOND appears to require dark matter itself—a considerable embarrassment for a theory that seeks to supplant the need for invisible mass.



Modified gravity. The spiral galaxy NGC 6946 with its rotation curve of velocity *V* versus distance *R* from the center (blue circles) (*14*). The green line is the rotation curve computed with Newtonian gravity. The gold line is the prediction of MOND. In both cases, the one unknown parameter of the computation, the stellar mass-to-light ratio, has been set to the value expected by stellar population synthesis models (*15*). MOND provides a good description of the data with no free parameters.

It is tempting to conclude that this is the real dark matter, some fundamentally new type of particle outside the highly successful standard model of particle physics. However, it might just be the result of another missing mass problem in extragalactic astronomy: the missing baryon problem. Our inventory of ordinary matter (baryons)—the stars and gas that we can see directly—falls well short of the amount we expect from big bang nucleosynthesis (*11*). Perhaps the unseen mass required in clusters by MOND is merely these dark baryons. Indeed, this has happened before. For a long time, astronomers thought that most of the ordinary mass in clusters was visible stars. Only relatively recently have we come to appreciate that all the stars in all the cluster galaxies are outweighed by a hot, diffuse gas between them. Still more baryonic mass may await discovery there.

The need for dark matter in clusters, even with MOND, was dramatically confirmed by the colliding "bullet" cluster (*12*). In this case the mass, as indicated by gravitational lensing, follows the galaxies rather than the gas. This implies that the unseen mass is in dense objects like brown dwarfs, but not diffuse gas. Although this provides some clue as to what the unseen mass is not, it does not tell us whether it is nonbaryonic dark matter or merely dark baryons. Moreover, although certainly puzzling for MOND, this case is also puzzling in the context of standard cosmology. The collision velocities of the components of the bullet cluster are extraordinarily high, a result much more natural to MOND than to conventional dark matter.

Another result more consistent with MOND than dark matter is the recent observation of mass discrepancies in tidal debris dwarfs (*13*). These dwarf galaxies form from the gas extruded from disks into long tidal tails as the result of collisions between massive galaxies. Because the orbits of dark matter and gas in disks are so different, these dwarfs are expected to be free of dark matter. Contrary to this expectation, they appear to show the familiar flat rotation curves.

This is precisely the behavior expected in MOND. In the conventional picture, however, we are obliged to invoke dark baryons in the disk in addition to the nonbaryonic dark matter in the halo. It is far from obvious that this can work, so the observations of Bournaud *et al*. (*13*) may pose an existential crisis for nonbaryonic dark matter.

Modern cosmology, with both dark matter and dark energy, has many genuine successes. So why should MOND work so well in describing rotation curves if, in fact, dark matter is their cause? We must understand this empirical phenomenology. If it is not the result of modified gravity, perhaps it is suggestive of something about the nature of dark matter.

If dark matter does exist in the form most commonly assumed, we should see it in the laboratory soon. Major experiments like the Large Hadron Collider and others have a good chance of detecting dark-matter particles in the near future. Moreover, measurement of a neutrino mass in excess of a few tenths of an electron volt would falsify the structure formation paradigm of standard cosmology, while perhaps going some way toward providing the missing mass in clusters with MOND. Regardless of how these experiments play out, there is clearly a great deal of fundamental physics left for us to learn. The universe may not be as cold and dark as we imagine.

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