factor NF-κB (*13*, *14*). TNFR2 and CD40 signal NF-κB activation more prominently than cell death. The cytoplasmic domains of these receptors associate with structurally related cytoplasmic proteins, TRAF1 and TRAF2, and, for CD40, also TRAF-3 (*15*). Fas signals apoptosis, mediated by the association of its cytoplasmic domain with a cytoplasmic protein, FADD. TNFR1, signals both apoptosis and NF-κB activation, mediated by the association of its cytoplasmic domain with the protein TRADD. TRADD associates with both TRAF2 and FADD, apparently accounting for the capacity of TNFR1 to activate both the apoptotic and NF-κB pathways. Interactions of TNFR1 and Fas with TRADD and FADD are mediated by a sequence motif known as a "death domain," present in all four proteins (*13*, *14*).

The recognition of a death domain motif within $p75^{NTR}$ led Rabizadeh *et al.* to examine whether $p75^{NTR}$ might promote apoptotic cell death. Evidence to support such an activity was obtained in several neuronal cell lines (*16*). Involvement of $p75^{NTR}$ in apoptotic cell death has also been reported for two populations of developing neurons (*17*). Enhanced conversion of sphingomyelin to ceramide, which accompanies TNF-induced apoptotic cell death, has been demonstrated in response to activation of $p75^{NTR}$ by NGF, BDNF, or NT-3 in several cell lines (*18*). The new study of Carter and co-workers extends these findings in an important way by directly demonstrating that $p75^{NTR}$ dramatically contributes to NF-κB activation and does so in a cell system that responds to NGF with a physiologically relevant response.

Two elements of functional complexity distinguish the neurotrophin response system from that of TNF. Firstly, NGF-induced tyrosine kinase activity of the TrkA receptor negatively regulates the capacity of $p75^{NTR}$ to mediate NGF-induced ceramide production. Thus, Trk function modulates $p75^{NTR}$ function, just as $p75^{NTR}$ function modulates Trk function. Second, although NGF binding to $p75^{NTR}$ induces ceramide production and NF-κB activation, BDNF and NT-3 binding to $p75^{NTR}$ do not induce NF-κB activation, but induce ceramide production even more effectively than does NGF. These results are difficult to understand if ceramide is the endogenous inducer of NF-κB activation, as is commonly presumed, and as Carter and co-workers assume in their new study. Recent studies suggest, however, that NF-κB activation is not downstream of ceramide production, but rather that ceramide production is a consequence of activation of ICE-like proteases in the alternative signaling pathway leading to apoptosis (*14*, *19*). A model that can reconcile these findings is one in which $p75^{NTR}$ signals through both FADD-like and TRAF-2–like pathways, with NGF activating both pathways, whereas BDNF and NT-3 activate only the TRAF-2–like pathway. The plausibility of nonequivalent action of the various neurotrophins is supported by the finding that an antibody against $p75^{NTR}$ inhibits NGF binding more effectively than binding of BDNF or NT-3 (*20*), suggesting that the neurotrophins bind to different sites on $p75^{NTR}$.

A key question remains: Do TRAF-2 and FADD themselves mediate $p75^{NTR}$ signaling, or are other structurally related proteins involved? The availability of dominant, negatively acting mutant forms of TRAF-2 and FADD will facilitate this analysis. The yeast two-hybrid technique has been instrumental in identifying signaling molecules interacting with other members of the $p75^{NTR}$-TNFR receptor family. It is likely that this approach will also help to unravel the $p75^{NTR}$ signaling system.

References

1. D. Johnson *et al.*, *Cell* **47**, 545 (1986); M. J. Radeke *et al.*, *Nature* **325**, 593 (1987).
2. B. D. Carter *et al.*, *Science* **272**, 542 (1996).
3. A. Rodríguez-Tébar, E. J. de la Rosa, A. Arribas, *Eur. J. Biochem.* **211**, 789 (1993); A. Rodríguez-Tébar, G. Dechant, Y. A. Barde, *Neuron* **4**, 487 (1990).
4. M. Barbacid, *J. Neurobiol.* **25**, 1386 (1994).
5. K.-F. Lee *et al.*, *Cell* **69**, 737 (1992); K.-F. Lee, K. Bachman, S. Landis, R. Jaenisch, *Science* **263**, 1447 (1994).
6. R. Klein, *FASEB J.* **8**, 738 (1994).
7. B. L. Hempstead *et al.*, *Nature* **350**, 678 (1991); A. M. Davies, K. F. Lee, R. Jaenisch, *Neuron* **11**, 565 (1993).
8. D. E. Wolf *et al.*, *J. Biol. Chem.* **270**, 2133 (1995).
9. P. A. Hantzopoulos *et al.*, *Neuron* **13**, 187 (1994).
10. A. H. Ross *et al.*, *Proc. Natl. Acad. Sci. U.S.A.* **81**, 6681 (1984); M. Taniuchi, H. B. Clark, E. M. Johnson Jr., *ibid.* **83**, 4094 (1986); Q. Yan and E. M. Johnson Jr., *Dev. Biol.* **121**, 139 (1987).
11. B. Seilheimer and M. Schachner, *EMBO J.* **6**, 1611 (1987); E. S. Anton *et al.*, *Proc. Natl. Acad. Sci. U.S.A.* **91**, 2795 (1994).
12. B. Beutler and C. van Huffel, *Science* **264**, 667 (1994).
13. M. Rothe, V. Sarma, V. M. Dixit, D. V. Goeddel, *ibid.* **269**, 1424 (1995).
14. H. Hsu *et al.*, *Cell* **84**, 299 (1996).
15. S. J. Baker and E. P. Reddy, *Oncogene* **12**, 1 (1996).
16. S. Rabizadeh *et al.*, *Science* **261**, 345 (1993).
17. G. L. Barrett and P. F. Bartlett, *Proc. Natl. Acad. Sci. U.S.A.* **91**, 6501 (1994); C. S. von-Bartheld *et al.*, *Neuron* **12**, 639 (1994).
18. R. T. Dobrowsky, M. H. Werner, A. M. Castellino, M. V. Chao, Y. A. Hannun, *Science* **265**, 1596 (1994); R. T. Dobrowsky, G. M. Jenkins, Y. A. Hannun, *J. Biol. Chem.* **270**, 22135 (1995).
19. G. J. Pronk, K. Ramer, P. Amiri, L. T. Williams, *Science* **271**, 808 (1996)
20. C. S. von Bartheld *et al.*, *J. Neurosci.*, in press (1996).

Saturn's Rings: Life at the Edge

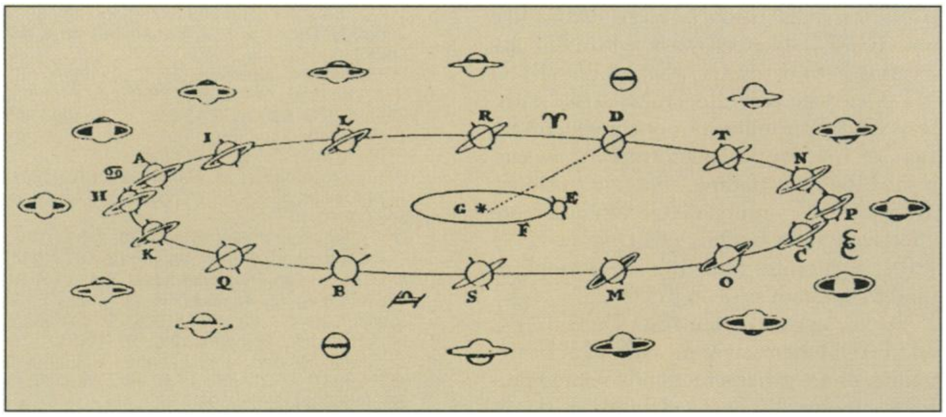
Carl D. Murray

The most spectacular ring system of the outer planets can also be a nuisance. The icy particles of Saturn's rings are so efficient at reflecting sunlight that the resulting glare makes it almost impossible to detect faint material lying close to the main ring system. However, over the last year astronomers were able to observe the Saturn system without the customary glare when the rings appeared edge-on as viewed from Earth. Some of the results obtained with the Hubble Space Telescope (HST) are reported in this issue (*1*–*3*). The most interesting images are those of the small satellites and ring features lying just beyond the main rings. They reveal a remarkably dynamic system with transient phenomena and a satellite inexplicably out of position. Something strange is happening.

It was Huygens (*4*) who first realized that Saturn's ring system appears to vanish twice every orbital period of 30 years as the Earth crosses the ring plane and the rings are viewed edge-on (see figure). As a result, ground-based discoveries in the Saturn system tend to occur at intervals of 14 or 16 years. Because our terrestrial viewpoint is changing as we orbit the sun, this last year has seen three Earth ring-plane crossings—22 May and 10 August 1995 and 11 February 1996—and one sun crossing on 19 November 1995. Although three spacecraft have now visited Saturn (Pioneer 11 and Voyagers 1 and 2), observations at times of ring-plane crossing are still vital, especially because they can provide unique viewing geometries for extended periods. For example, Hall *et al.* (*1*) discuss the spectroscopic detection of OH immediately above the main rings, an observation that can only be made at times of ring-plane crossing.

A recurring yet unexpected result common to many of the current observations is the importance of Saturn's F ring in attempts to understand phenomena as varied as the thickness of the rings and the temporary nature of some features. The F ring is a narrow, multistranded ring lying 3400 km beyond the edge of the main ring system

The author is in the Astronomy Unit, Queen Mary and Westfield College, University of London, London E1 4NS, UK. E-mail: C.D.Murray@qmw.ac.uk.



The geometry of Saturn's ring plane crossing. From Huygens's *Systema Saturnium* published in 1659. Huygens correctly deduced that Saturn "is surrounded by a thin, flat ring, nowhere touching, and inclined to the ecliptic." As Saturn moves around its orbit the aspect of the rings (outermost drawings) changes. G is the sun, E the Earth, and F the Earth's orbit. Twice per Saturn orbit, at positions B and D, the rings appear edge-on.

and exhibited a clumpy and braided structure in several Voyager images. It has never been detected in ground-based observations and yet is clearly visible as a bright ring in the stunning HST images (*2*, *3*). The residual brightness of the edge-on rings leads to estimates of their effective or photometric thickness, although this may be masked by local or global warping of the rings. Previous Earth crossings in December 1966 and March 1980 suggested an effective thickness of 2.4 ± 1.3 km and $1.1^{+0.9}_{-0.5}$ km, respectively (*5*). Nicholson *et al.* (*3*) used the HST to measure a value of 1.2 to 1.5 km but recognize that the F ring, rather than the main rings, dominated their signal at the August crossing. Because theoretical estimates of the true thickness of the rings are smaller than the HST measurement by at least a factor of 10, the F ring probably does an excellent job of masking the edge-on view of the main rings. A slight inclination of the F ring to the equatorial plane may also explain why the exact times of crossing at the east and west ansae are different (*3*). Unfortunately, this difference means that it will be more difficult to use such timings to measure the precession of Saturn's rotation axis (*6*).

The majority of Saturn's 18 moons were first detected at times of ring-plane crossing, so more discoveries were expected during the 1995–1996 events. What is surprising is that four of the six new objects observed by Bosh and Rivkin (*2*) and Nicholson *et al.* (*3*) are thought to be arcs or clumps of material in the general vicinity of the F ring. The F ring is strange, even for a planet surrounded by strange rings. Although the Voyager spacecraft did not obtain complete longitudinal coverage of the ring at high resolution, there is little doubt that there were fundamental changes in the ring in the 9 months between the two Voyager encounters. Bright arcs of material could be seen at both encounters, but the complicated, twisted appearance in the Voyager 1 images was replaced by an altogether more regular ring by the time Voyager 2 arrived. Now the HST images are showing changes between the May, August, and November observations. Although some of the structure in the ring is known to be caused by the gravitational effect of Prometheus, a small moon orbiting between the F and A rings, there is still no explanation for most of the features seen in the Voyager and HST images. However, Prometheus is presenting some problems of its own.

The orbits of a number of small satellites moving close to the edge of the main rings were determined with the use of Voyager observations, but the HST data shows that two of these satellites—Atlas and Prometheus—are out of position. Atlas, which lies just 100 km beyond the edge of the A ring, was detected by Bosh and Rivkin (*2*) but 25° ahead of its expected position; this discrepancy may be the result of a poorly determined Voyager orbit. On the other hand, Prometheus's orbit was expected to change because an exchange of angular momentum with material in the A ring. A slight expansion of its orbit should have occurred, but the HST observations (*2*, *3*) show Prometheus lagging behind its expected position by a remarkable 20°, two orders of magnitude larger than the predicted lag. It has been suggested (*7*) that this could be caused by collisions between Prometheus and the F ring, which should occur every 19 years. However, the fact that the lag did not change significantly between the various detections in 1995 appears to rule out a single collision and puts severe restrictions on any collisional model. Even the promising proposal (*7*) that 1995 S7, one of the features discovered by HST, could be responsible for perturbing Prometheus's orbit is confounded by prediscovery measurements in 1966 (*8*). The satellite is not where it should be and this is still not understood.

Other satellites are known to be involved in producing ring structure. For example, Mimas, a 400-km-diameter saturnian moon with an orbital inclination of 1.5° is known to produce corrugations at certain locations in the A ring; its perturbations also determine the outer edge of the B ring. Paradoxically, it is the gravitational effect of the small satellites orbiting close to the rings that may determine the ultimate fate of the entire ring system. The exchange of angular momentum between these satellites and ring particles will cause the rings to spiral in toward the planet, giving an estimated ring lifetime of only 10^8 years; this implies that ring systems may be temporary adornments to the outer planets. One of the goals of the HST observations was to confirm this uncomfortably short lifetime by measurements of the small lags in the positions of these satellites. The best hope was to use Prometheus, the most massive of the close satellites and therefore the one producing the biggest effect. However, unless it is possible to understand and model whatever is happening to Prometheus, especially if collisions are involved (*7*), these attempts will fail and less promising satellites will have to be used for such measurements.

In the last century, James Clerk Maxwell (*9*) summed up the dynamical problems posed by Saturn's ring system: "We must either explain its motion on the principles of mechanics, or admit that, in the Saturnian realms, there can be motion regulated by laws we are unable to explain." What is required in order to understand the F ring and its realms is an in situ view of the system as it evolves. Fortunately, the Cassini spacecraft will be launched next year and will start its 4-year orbital tour of the Saturn system in 2004. A comforting result from the HST observations (*3*) is confirmation that the extended, diffuse E ring that Cassini will fly through repeatedly is composed of micrometer-sized particles that will not pose a significant hazard to the spacecraft. Cassini is our best chance yet to understand this complicated region. Life at Saturn's edge is bewildering, but it is also exciting and full of surprises.

References

1. D. T. Hall, P. D. Feldman, J. B. Holberg, M. A. McGrath, *Science* **272**, 516 (1996).
2. A. S. Bosh and A. S. Rivkin, *ibid.*, p. 518.
3. P. D. Nicholson *et al.*, *ibid.*, p. 509.
4. C. Huygens, *Systema Saturnium* (1659).
5. A. Dollfus, *Astron. Astrophys.* **75**, 204 (1979); B. Sicardy *et al.*, *ibid.* **108**, 296 (1982).
6. R. French *et al.*, *Icarus* **103**, 163 (1993).
7. C. D. Murray and S. M. Giuliatti Winter, *Nature* **380**, 139 (1996).
8. C. F. Yoder, S. P. Synnott, H. Salo, *Astron. J.* **98**, 1875 (1989).
9. J. C. Maxwell, *On the Stability of the Motion of Saturn's Rings* (Macmillan, London, 1859).