the chimpanzee lineage has no fossil record whatsoever. One explanation has been that chimpanzees have always lived in forested environments, and that forest creatures are rarely preserved as fossils. Hominids only become (relatively) abundant as fossils after they moved from forests to more open habitats. However, this argument is turned on its head by strong evidence that Orrorin ${ }^{3}$ and Ardipithecus ${ }^{7}$ lived in woodland. The fossils of animalssuch asmonkeys and small antelopes found alongside the hominids, as well as palaeobotanical and isotopic evidence, suggest that Ardipithecus lived in a relatively well-forested and high-altitude environment. Indeed, thiscreaturemay have been confined to such a habitat: as WoldeGabriel and colleagues ${ }^{7}$ show, searches for early hominids in geological settings indicative of the open-country habitats associated with later hominids were less rather than more likely to produce results. So it may be that hominids were woodland creatures until about 4.4 million years ago ${ }^{8,13}$.

Given that chimpanzees today live in environments rather like those inhabited by Ardipithecus and Orrorin, could it be that at least one of these early hominids is actually more akin to chimpanzees? Questions have been raised about the status of Orrorin as a hominid ${ }^{5,6}$. For their part, Senut and colleagues ${ }^{2}$ defend thehominid status of Orrorin and proposethat Ardipithecus is an ancestor of chimpanzees. But they do not discuss the implications of this view for the history of chimpanzees, as distinct from that of hominids.

Sadly, I doubt that the status of these
creatures can be resolved to general satisfaction. Some researchers have suggested ${ }^{14}$ that the dental and skeletal traits conventionally used as the basis for hominid systematics are unreliable guides for reconstructing evolutionary history, in that the phylogenies created using these traits differ from thosebased on molecular information from living primates. Given that bones and teeth are, for practical purposes, all there is to go on, uncertainty is likely to reign for some time, leaving the nature of the latest common ancestor - and the general course of early hominid evolution - as mysterious asever.

Is the outlook completely gloomy? Perhapsnot. The accumulating data on pal aeoenvironments should at least improve our understanding of the lives and times of early hominids (and perhaps of early chimps), even though the evolutionary relationships remain murky.
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## Planetary science

# Saturn saturated with satellites 

Douglas P. Hamilton
Advances in detector technology have led to a rash of newly discovered moons around the giant planets. Saturn currently has the most known satellites - but for how long?

Parents of small children are expected to know the answers to questions like "Which planets in the Solar System havethemost moons?" But asurgeof discoveries of distant planetary companions in the past five years has left beleaguered parents everywhere hard pressed to answer this query correctly. Today, the planets with the most known natural satellites are Saturn with 30 moons, Jupiter with 28 , Uranus with 21 and Neptunewith 8. Butthislist had adifferent order last year, and was different again the year before that. Not since the Voyager fly-bys of the 1980s have so many moons been discovered so quickly. On page 163 of this issue ${ }^{1}$, an international team of astronomers led by Brett Gladman announces the
discovery of a dozen new kilometre-sized satellites - the culmination of their highly successful observations of Saturn.

Thenew discoveries have comenot from telescopes in space, nor from the largest telescopes on Earth, but rather from mediumsized ground-based instruments (3-5 m diameter), which can efficiently scan large regions of thesky. Ground-based surveysare sensitive to small moons far from planets, butfail to spot nearby satell ites owingto light scattered from theplanet. They complement spacecraft measurements, which can easily find small moonlets close to their parent planet, but cannot efficiently search for distant satellites.

Rapid improvementsin detector technol-
ogy have made systematic ground-based searches much more tractable than even a decade ago. Today, digital CCD (chargecoupled device) arrays with $10,000 \times 10,000$ pixels can cover a quarter-squaredegree patch of sky (roughly equivalent to the area of thefull Moon) in asingleexposure. Equally important are improvements in computers, which allow data to be analysed in real time, and the development of sophisticated algorithms that can automatically detect faint, slowlymovingobjects.

Despite these improvements, finding small satellites is still a daunting task. The region of space that needs to be covered in a thorough search is a planet's'Hill sphere' the area within which satellites can orbit stably. Theprojected area covered by the H ill sphere is determined by the planet's mass: for Jupiter, Saturn, Uranus and Neptune, theseareas are $48,22,6$ and 7 square degrees, respectively. Even with a quarter-squaredegreefiel d of view thereisalot of spaceto be covered and, partly for this reason, Gladman and colleagues focused first on moredistant Uranus and Neptune ${ }^{2,3}$ beforeproceeding to Saturn ${ }^{1}$. To cover Saturn's entireH ill sphere, Gladman et al. planned a careful systematic campaign involving multipletelescopes and coordinated follow-up observations.

Remarkably, thisnew survey covered Saturn'sentireHill spheredown to abrightness limit of 23 rd magnitude ${ }^{1}$. This means that, with reasonable assumptions for the reflectivities of the new moons, Gladman et al. havefound all of theobjects with radii larger than about 4 km thatarecirclingSaturn (Fig. 1). They estimatethat their previous studies of Uranusand Neptune arenearly complete, covering about 90\% of the Hill spheredown to a similar brightness ${ }^{3}$. Although a complete survey of Jupiter's environs has not yet been undertaken, an impressive step in this direction was made earlier this year by Sheppard et al. ${ }^{4}$, who added ten new moons to theonedetected last year ${ }^{5}$.

Because they shineby reflectingsunlight, satellites of equal brightness (23rd magnitude) around Jupiter, Saturn, Uranus and Neptune have very different radii: approximately $1,4,16$ and 36 km , respectively. This makes it difficult to compare different satellite populations because the observations discriminate against the more distant planets. For example, all thenew saturnian satellites are probably too small to have been detected if they had orbited Uranus or Neptuneinstead. Similarly, a group of three very faint objects that Gladman et al. ${ }^{1}$ spotted moving near Saturn but then lost - when angling for moons, unlike when angling for fish, it is the small ones that get away would have been more easily tracked had they circled Jupiter instead.

N onetheless, complete surveys of satellite populations around individual planets can reveal important clues to theorigin and

early history of theplanets. Indeed,Gladman et al. observe that Saturn's moons are grouped into distinct families (Fig. 1) with similar orbital properties, just like asteroids and distant satellites of Jupiter. Families are thought to be formed either during cratering collisions that break fragments off parent bodies, or during more violent catastrophic collisions that completely destroy theparent.

Although the current orbits of the satellites (Fig. 1) hint at these relationships, clearer indications comefrom similarities in their long-term orbital properties (particularly the average tilt of the orbital plane) ${ }^{1}$. Theexistenceof satellitefamiliesimpliesthat there are substantial unseen populations of smaller bodies around all the giant planets, because collisions that chip 1-km fragments off $10-\mathrm{km}$ moons occur far more frequently than collisions that produce $10-\mathrm{km}$ fragments from $100-\mathrm{km}$ moons. The three little onesthat got away near Saturn arejust thetip of theiceberg.

If each satellite family was derived from a single parent moon, where did the parents originate? It haslong been beli eved that satellites were captured from independent orbits around the Sun early in the history of the Solar System. At that time, the Solar nebula, a large disk of gas and dust, still surrounded theSun, and smaller disks circled each of the gaseous planets. There are several possible capture mechanisms involving interactions with the planet's gaseous nebula ${ }^{6}$, collisions with other objects within the planet's Hill sphere ${ }^{7}$, and expansion of the Hill sphere as the planet grows in size $e^{8}$. Although these mechanisms for capture have been investigated, the details arenot well understood and the process of satellite capture remains an outstanding problem in planetary science.

The next observational challenge is a survey of Jupiter's entire Hill sphere down to 23 rd magnitude. Such a survey is complicated by the large search area (more than for the other three giant planets combined), the potentially huge number of detectable 1-km-sized moonlets, the more rapid orbital motion of jovian satellites, and thegreater likeli hood of mistaking them for main-belt asteroids. N onetheless, a multitude of jovian satellites probably lurk undetected in the vast region of space controlled by this giant planet. It will not be long before massive Jupiter regains

Figure 1 The current orbits of the outer satellites of Saturn. The radius of the Hill sphere is about 65 million km , which is equal to 1,100 Saturn radii, or 0.43 AU ( 1 AU is the mean Earth-Sun distance). Saturn is at the centre and the white objects on inner, nearly circular, prograde orbits are the classical satellites: Titan, Hyperion and lapetus. Prograde objects circle Saturn in the same way as its classical satellites (anticlockwise when viewed from above), whereas retrograde objects orbit in the opposite direction (clockwise). The 12 new satellites discovered by Gladman et al. ${ }^{1}$ can begrouped into families according to their orbital properties: cyan and green objects are the new prograde groups, whereas pink and red dots (including previously known Phoebe) are all retrograde satellites. Animations of these and all other Solar System satellites can be found at ref. 9 .
thetitleof theSolar System's most-mooned planet.
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## Apoptosis

## Mostly dead

Douglas R. Green and Helen M. Beere
It has always been thought that once the process of cell suicide has passed a certain point, it is irreversible. Yet it seems that cells can recover - but only if they are not eaten by nearby 'phagocytic' cells.

In all animals, the process of programmed cell suicide (apoptosis) is coordinated by enzymes known as caspases, which cut up key substrates in the cell. The dying cell is then neatly packaged, engulfed by neighbouring 'phagocytic' cells, and cleared from the body without fanfare, leaving no evidence of the catastrophic events that preceded. It has always been assumed that there is a'point of no return' in this death cascade - at or shortly before the time at which caspases are activated - beyond which the process of cell execution proceeds inexorably. This view is challenged by Reddien et al. ${ }^{1}$ and Hoeppner et al. ${ }^{2}$ on pages 198 and 202 of this issue. It seems that cells in which
caspases have been activated can in fact progress through a state of being 'mostly dead', a stage that physically resembles the early phaseof apoptosis but from which cells can fully recover.

During the development of the nematode worm Caenorhabditis elegans, 131 cells are destined to die by apoptosis. These cell deaths depend on the presence of a caspase, CED-3, and on a moleculecalled CED-4 that binds to and activates CED-3. In healthy cells, CED-4 is maintained in a functionally inactive state by its association with CED-9. The trigger for cell death is the protein EGL-1, which is expressed in response to developmental cues. EGL-1 bindsto CED-9,

