of mutations into four different tRNAs that normally specify four distinct amino acids. These changes allowed each of the tRNAs to be charged with both their own particular amino acid and the other three amino acids. At the same time, care was taken to ensure that the changes introduced into the tRNAs did not disturb their interactions with EF-Tu. The investigators ended up with 16 aa-tRNAs, of which 12 were mischarged species.

When the affinities (dissociation constants) of the 16 aa-tRNAs for EF-Tu were determined, the results were surprising, to say the least. Although correctly charged aa-tRNAs all bound to EF-Tu within a 10-fold range of affinities, the complete data set encompassed a 5000-fold difference in binding. The significance of this range of affinities is illustrated by the fact that uncharged $tRNA^{Phe}$ only binds to EF-Tu 1000 times less tightly than the corresponding charged species $Phe\text{-}tRNA^{Phe}$ (*8*). Closer examination of the behavior of particular mischarged aa-tRNAs suggests how EF-Tu might exploit these large differences in substrate binding to ensure the fidelity of protein synthesis. Although some mischarged aa-tRNAs bind to EF-Tu with less affinity than their correctly charged counterparts, surprisingly, some bind considerably more tightly. At first sight, a strong affinity for EF-Tu does not seem to be the best way to prevent delivery of a mischarged aa-tRNA to the ribosome. But, as LaRiviere *et al.* explain, both very tight and very weak binding could compromise the efficient delivery of an aa-tRNA to the ribosomal A-site (see the figure). Previous studies indirectly suggest that mischarged aa-tRNAs that bind tightly to EF-Tu would be less abundant in the cell, thus confining discrimination by EF-Tu to weakly binding mischarged species.

Perhaps the most immediate question raised by the LaRiviere *et al.* data is how EF-Tu manages to discriminate the 20 correctly charged aa-tRNA isoforms in the cell from the 380 mischarged species. This problem of molecular recognition is compounded by the fact that the 380 mischarged species simply represent different combinations of the same tRNA and amino acid moieties present in the 20 correctly charged aa-tRNAs. The answer suggested by LaRiviere *et al.* is that EF-Tu uses a form of "combinatorial" recognition. After they analyzed the individual contributions of the amino acid and tRNA moieties to the overall binding energy, it became clear that the two parts of an aa-tRNA could be broadly divided into "tight" and "weak" EF-Tu binders. The key point with regard to recognition is that the combination of a tight and weak partner in a correctly charged aa-tRNA results in the groups thermodynamically compensating for each other, enabling effective binding of the aa-tRNA to EF-Tu (see the figure). On the other hand, mischarged aa-tRNAs generally seem to contain two groups that are either both tight binders or both weak binders. Thus, mischarged aa-tRNAs bind to EF-Tu too ineffectively for subsequent delivery to the ribosome. The data do yield a few exceptions to this rule, but these should be clarified once this approach is expanded to include more aa-tRNAs. Sampling of other aa-tRNAs should also help in the interpretation of tight and weak binding events in terms of known structures of EF-Tu, particularly for the recognition of the tRNA moiety (*7*, *9*).

The LaRiviere *et al.* study provides compelling evidence that EF-Tu can differentiate correctly charged from mischarged aa-tRNAs. Together with earlier findings showing that EF-Tu associates with other components of the translation machinery (*10*), possibly promoting aa-tRNA delivery to the ribosome, the LaRiviere work makes it clear that describing EF-Tu as a nonspecific carrier is incorrect. Whatever the final mechanistic details, it now appears that EF-Tu is a critical component of the stringent quality-control machinery that ensures the accurate translation of mRNA into protein.

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PERSPECTIVES: PLANETARY SCIENCE

Jupiter and Its Moons

David J. Stevenson

We live in an exciting time for people who care about the origin of planets. New planets and planetary systems are discovered regularly (*1*) and can be compared with our own solar system. In our solar system, the Galilean moons that orbit Jupiter form a planetary system that is also coming into focus, thanks to the remarkable success of the Galileo mission (*2*).

How did these planetary bodies form? We do not yet have a fully satisfying answer to this question, but a story is emerging that differs from the formation of the solar planets and from the formation of Earth's moon. In this multiplicity of origins, the Galilean moons emerge as a last gasp in the formation of Jupiter. Their formation may have postdated the accumulation of nearly all of Jupiter's mass and took place over a period of millions of years—surprisingly long for bodies that orbit their parent once every few days.

Galileo discovered the four moons that bear his name (*3*) in January 1610. In those days, one could publish rapidly (*4*). Already in March 1610, Galileo wrote in *Sidereus Nuncius* that "I should disclose and publish to the world the occasion of discovering four Planets never seen from the beginning of the world up to our own times. I summon all astronomers to apply themselves to examine and determine their periodic times." Galileo understood the cosmological importance of his discovery, which provided key evidence in support of the Copernican system and showed that not all heavenly bodies revolve around Earth. However, appreciation of what the Galilean satellites might tell us about planet formation took much longer and is still ongoing.

There are many similarities between the Jovian system and our solar system. Both systems are extremely regular. Bodies orbit in a nearly common plane—Jupiter's equatorial plane for the Galilean satellites and the Sun's ecliptic plane for the solar system. In both cases, bodies orbit in a prograde sense (anticlockwise when viewed from above), with orbits spaced in approximate geometric progression. The total mass of Jupiter's satellites is about the same as that of Mars and probably about 1% of the heavy-element mass (everything except hydrogen and helium) inside Jupiter. This is a similar ratio to the heavy-element distribution in our solar system, where the Sun contains around 10 Jupiter masses and the planetary system tens of Earth masses of heavy elements.

Yet there are also striking differences. The solar system is spread out relative to the size of the Sun, with even the Sun-hugging

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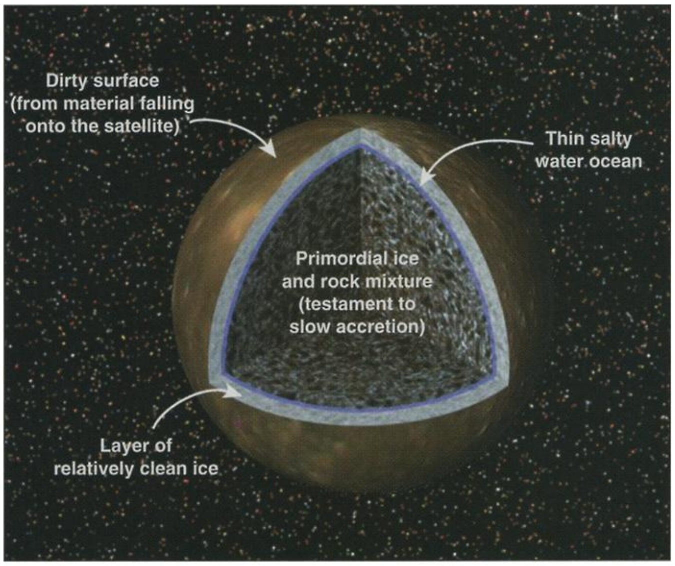
Earth over 200 solar radii away, whereas the most distant Galilean satellite, Callisto (see the top figure), is less than 30 Jupiter radii from Jupiter. The compactness of the Jupiter system undoubtedly arises from the limited size of the region in which Jupiter is gravitationally dominant over the Sun.

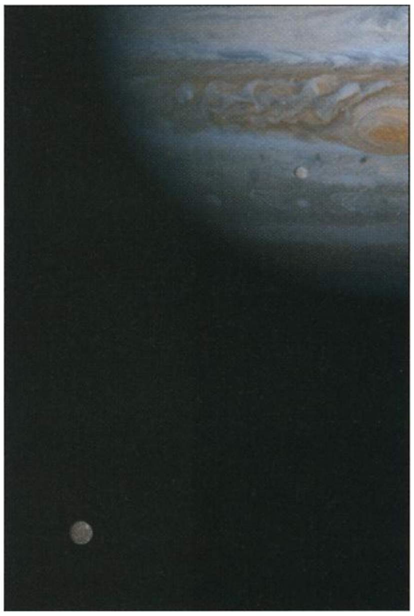
The Galilean satellites are remarkably similar in size and exhibit a compositional trend (*5*) that suggests higher temperatures or a higher energy environment close to Jupiter at the time of formation. From the innermost orbit outward, Io is rocky, Europa is rocky but with some ice, and Ganymede and Callisto are half rock, half ice by mass. For both Earth and Ganymede, $GM/RL \sim 1$, where G is Newton's gravitational constant, M is the mass, R is the radius, and L is the appropriate latent heat of vaporization (rock for Earth and water ice for Ganymede). Gravity thus played an important and comparable role in influencing thermodynamic change (melting, vaporization, and differentiation) in these otherwise disparate bodies.

It is tempting to suggest an origin for the Galilean moons that is similar to the formation of the solar system. The latter is thought to have formed through the collapse of an interstellar cloud of gas and dust in 10^5 to 10^6 years, followed by an aggregation process that took tens of millions of years in the case of Earth (*6*). This model only makes sense, however, if the collapse time is short compared with the accumulation time. In the Galilean satellite system, the accumulation time would then have been a mere 10^4 years or so because it scales with the orbital time, which is very short for the Jovian moons. However, the delivery of material from the solar nebula into Jupiter's sphere of influence probably took a million years or more (*7*). The Jovian system therefore cannot have formed in a similar way to the solar system.



The interior of Callisto. Gravity measurements by the Galileo spacecraft suggest that this moon has only partly segregated into ice and rock, suggesting that it accreted very slowly.

Independent evidence for such a different mechanism comes from the Galileo measurements of Callisto's gravity (*8*). The results indicate that the distribution of mass is less centrally concentrated in Callisto than in Ganymede and that only partial separation of rock from ice occurred in Callisto (see the bottom figure). This means that this moon must have formed very slowly, over a million years or more, because the heat generated by faster accretion would melt the ice, leading to facile separation of water and ice from rock.



Jupiter and Callisto

Such slow and gentle satellite accumulation is best accomplished at the end of Jovian accretion. At that time, Jupiter had collected most of its gas but had probably created a "gap" (a region of greatly reduced gas density) in the adjacent solar nebula (*7*). Some solids and gas would still be delivered during this protracted epoch, leading to the formation of a disk around Jupiter, with a net prograde angular momentum dictated by the gas inflow. Enough solid material must have been delivered to the particulate and gas disk to explain the total satellite mass, but it is neither necessary nor desirable that the solid portion of the disk contained more than a small fraction of this mass at any instant. An earlier epoch of faster mass delivery and satellite formation may have occurred with those pre-Galilean satellites swallowed up by the growing Jupiter. Ideas like this are not fully developed but were part of some presentations made at a recent Jupiter conference (*9*).

The most popular idea for formation of our moon involves a delivery time that is short compared with the accumulation time, but in that case, "delivery" of material splashed out from a giant impact into Earth's orbit would take just a few days or less (*6*). Our solar system, the Jovian system, and the Earth-Moon system thus seem to have distinctively different dynamics. Nevertheless, many of the processes thought to be important in the solar nebula (including those thought to be responsible for orbital migration in other solar systems) and the protolunar disk may have also played a role in the Jovian system.

We have limited knowledge of the compositions of the satellites and the thermal regimes at their time of formation. Do the satellites bear the signature of the solar nebula, or were their compositions greatly altered by processes in the Jovian environment? Europa may have had a naked ocean (without an overlying ice shell) in this earliest epoch if there was sufficient water on the surface and if early Jupiter was as luminous as models suggest.

The Galilean satellites are a planetary system as exciting to visit and understand as our solar system, even without the current obsession with the possibility of life on Europa. Hopefully, future missions will include orbiters around all large Jovian satellites.

References and Notes

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