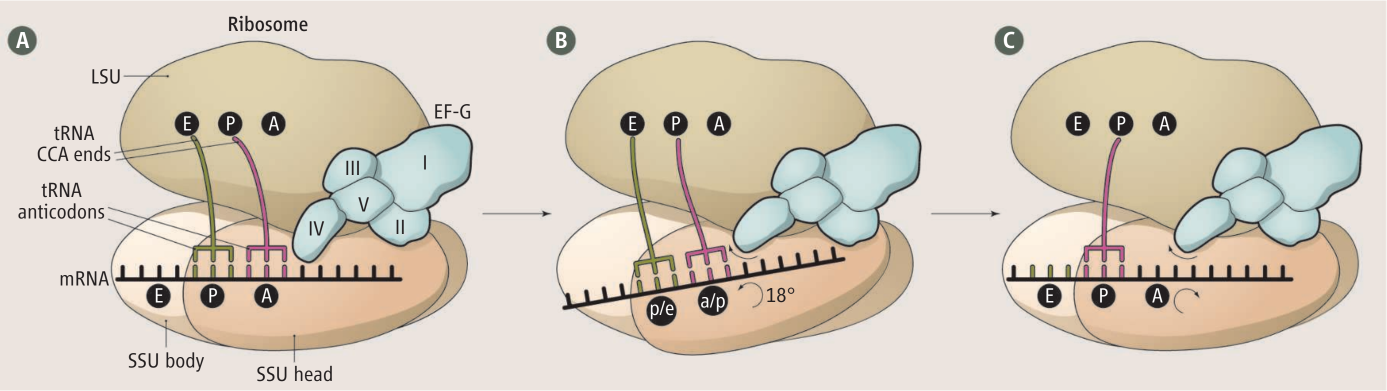

Translocation dynamics. (**A**) In the pretranslocation state of the ribosome, the tRNA anticodons are located in the A and P sites on the SSU, while the tRNA CCA ends oscillate between the A and P or P and E sites on the LSU. EF-G is in the GTP-bound conformation. (**B**) In the intermediate state of translocation, derived from the new crystal structures (*1*–*3*), the rotation of the SSU head domain brings the tRNA anticodons and the mRNA codons into a state intermediate between A and P (called a/p) or between P and E (p/e) on the SSU. Domain IV of EF-G moves. (**C**) In the posttranslocation state (*4*, *14*), only one tRNA is bound to the ribosome in the P site, the E-site tRNA is released, the SSU head domain is rotated backward, and EF-G has changed the conformation further before it dissociates from the ribosome (*1*–*3*).

of movement, and the new structures suggest how this is achieved. EF-G domain IV, which is essential for tRNA and mRNA translocation (*10*, *11*), projects into the A site, thereby preventing the backward movement of the tRNA (*1*–*3*) (see the figure, panel C). In addition, elements of 16*S* ribosomal RNA in the SSU act as molecular pawls to fix the position of the mRNA, preventing backward movement of the mRNA (*3*).

The structures also show how GTP hydrolysis in EF-G may be activated by the ribosome. In the structures by Tourigny *et al*. (*1*) and Pulk and Cate (*2*), the conserved histidine residue from switch 2 is poised for hydrolysis. By contrast, in the structure by Zhou *et al*. (*3*), this histidine is too far from the γ-phosphate to act in catalysis, suggesting that a nonactivated intermediate was trapped. Mutations of the histidine residue in either EF-G or EF-Tu, another translational GTPase, abolish GTP hydrolysis and block the progression through the translation elongation cycle (*9*, *12*), consistent with a catalytic role of the histidine. Key residues in EF-G and EF-Tu (*13*) form a nearly identical catalytic site, suggesting a common mechanism for the activation of translational GTPases by the ribosome.

The mechanism of translocation represents a case study of directed movement in large molecular machines. The new structures (*1*–*3*) suggest how GTP hydrolysis is coupled to translocation. The mechanism of coupling is reminiscent of motor proteins using ATP hydrolysis to drive directed movements (*2*). A remaining challenge is to determine the structure of a true pretranslocation complex (with tRNAs bound to both P and A sites and without EF-G occupying the A site of the SSU) and of intermediate states of translocation. Another key question is how EF-G accelerates translocation. Answering this question will require comparison of intermediate states of EF-G–catalyzed and spontaneous translocation.

References

1. D. S. Tourigny, I. S. Fernández, A. C. Kelley, V. Ramakrishnan, *Science* **340**, 1542 (2013).
2. A. Pulk, J. H. D. Cate, *Science* **340**, 1544 (2013).
3. J. Zhou, L. Lancaster, J. P. Donohue, H. F. Noller, *Science* **340**, 1543 (2013).
4. J. Frank, R. K. Agrawal, *Nature* **406**, 318 (2000).
5. B. S. Schuwirth *et al*., *Science* **310**, 827 (2005).
6. D. Moazed, H. F. Noller, *Nature* **342**, 142 (1989).
7. N. Fischer, A. L. Konevega, W. Wintermeyer, M. V. Rodnina, H. Stark, *Nature* **466**, 329 (2010).
8. A. H. Ratje *et al*., *Nature* **468**, 713 (2010).
9. C. E. Cunha *et al*., *Translation* **1**, e24315 (2013).
10. M. V. Rodnina, A. Savelsbergh, V. I. Katunin, W. Wintermeyer, *Nature* **385**, 37 (1997).
11. A. Savelsbergh, N. B. Matassova, M. V. Rodnina, W. Wintermeyer, *J. Mol. Biol.* **300**, 951 (2000).
12. T. Daviter, H. J. Wieden, M. V. Rodnina, *J. Mol. Biol.* **332**, 689 (2003).
13. R. M. Voorhees, T. M. Schmeing, A. C. Kelley, V. Ramakrishnan, *Science* **330**, 835 (2010).
14. Y. G. Gao *et al*., *Science* **326**, 694 (2009).

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PLANETARY SCIENCE

Solving the Mascon Mystery

Laurent G. J. Montesi

Modeling the formation of regions of mass concentration may lead to new estimates of early heat flux in the Moon.

When we look at the Moon, we can see images of a man, a rabbit, and countless other analogies. These images are the figments of our imagination, inspired by the distribution of thick lava sequences, the mare basalts, that fill ancient basins that formed by large meteorite impacts early in solar system history. Still, mysteries remain hidden beneath the lunar surface. The first spacecraft in orbit around the Moon felt a stronger pull of gravity when passing over these basins, implying that a mass concentration, or "mascon," was present there (*1*). Subsequent studies added to the puzzle of mascons and provided partial explanations for their formation (*2*–*4*). On page 1552 of this issue, 45 years after the initial discovery, Melosh *et al*. (*5*) put all the pieces together and provide the first self-consistent model for the origin of mascons.

At first sight, the existence of mascons seems incompatible with the origin of the lunar basins in which they form. The impact process excavates a hole in the lunar crust and upper mantle, resulting in a mass deficit, not a mass concentration. The lunar mantle flows toward the basin interior and reduces the initial mass deficit. However, this flow process, which is similar to the rebound of

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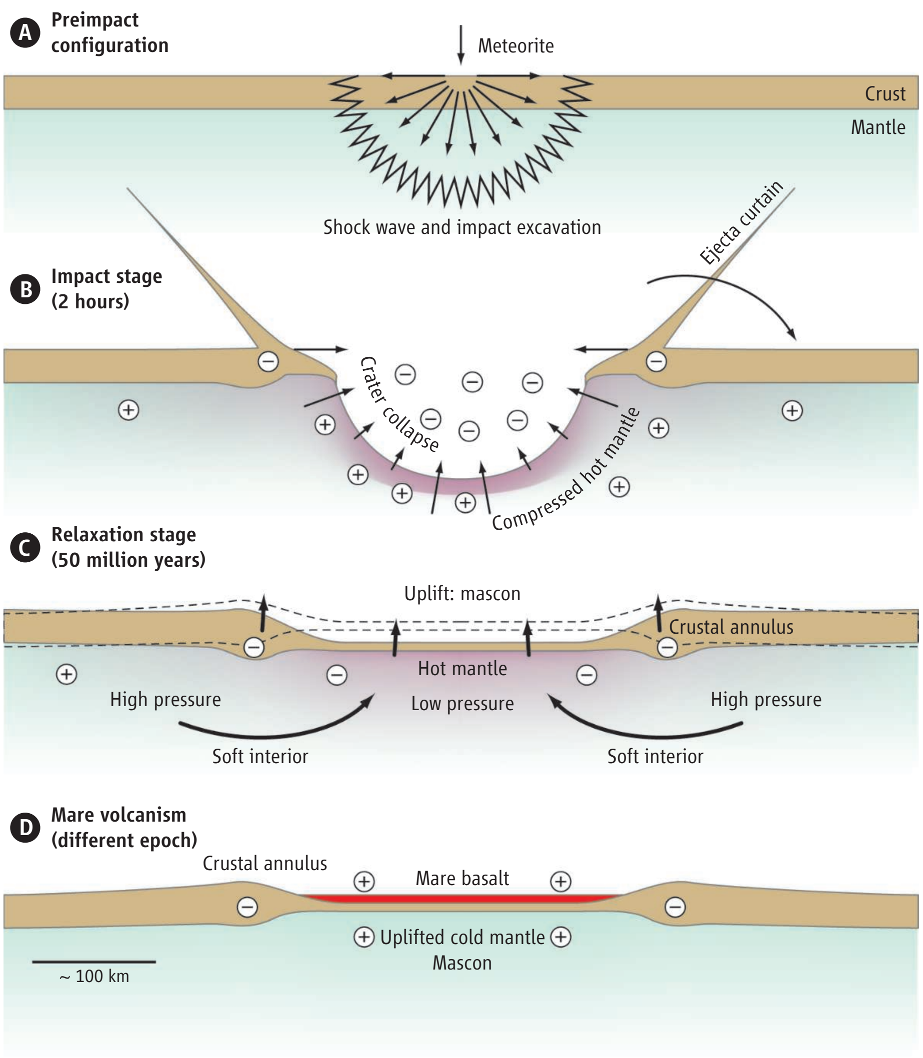

Mascon development. (**A**) A meteorite impact shocks the mantle and excavates a cavity that rapidly collapses while (**B**) depositing a curtain of crustal material that thickens the crust in an annulus at the edge of the basin. (**C**) Both the crust annulus and the shocked mantle drive mantle flow that uplifts the basin and forms a mascon. (**D**) Later mare basalts may add to the mass anomaly. The plus and minus symbols represent density anomalies over the initial configuration in (A).

Earth's mantle after the removal of ice caps at the end of the last glacial age, slows down as the mass anomaly decreases. How can a mass deficit in the basin turn into a mass excess?

As mare basalts are too thin to explain the mass excess, it was proposed that the mantle bounces above its isostatic level and is frozen in place (*3*, *6*). Melosh *et al.* show that this dynamical process is not needed. Mascons can instead form as the result of slow mantle flow driven by two low-density regions generated by the impact process—an annulus of thick, low-density crust, and a low-density mantle under the basin (see the figure).

Both density anomalies drive uplift of the basin. However, the surface cools rapidly, essentially freezing in the contrast between the low-density crustal annulus and the high-density basin interior. Deep-seated density differences continue to drive mantle flow, lifting the entire basin. The impact basin as a whole may end up being compensated (with deep density anomalies balancing out the surface mass deficit), but the frozen structure inside the basin produces a low-density ring surrounding the high-density interior, which forms a mascon.

Although none of the processes present in this model are fundamentally new, Melosh *et al.* put them all together in a start-to-finish model. The formation of a mascon hinges on the delicate balance between the strength and thermal structure of the lunar crust and upper mantle. The crust must be cold and strong enough to form and maintain a crustal annulus. The deeper mantle must be cold enough to relax over time scales much longer than that of the initial cooling of the surface yet not so strong that it shears the crustal annulus away. The importance of the work by Melosh *et al.* is, therefore, not only that a mascon appears in this model but that it provides constraints on the conditions under which mascons can form.

The geological activity of planets and moons has changed dramatically during solar system history. Ancient volcanic activity shows that the interiors of the Moon, Mars, and Mercury were hotter 4 billion years ago than they are today. However, that heat is long gone. Ancient heat flux is usually estimated by matching the length scale of tectonic deformation (*2*, *7*–*9*). Melosh *et al.* show that a mascon forms when the lunar heat flux is relatively high, with a surface geotherm of 30 K/km. It may now be possible to use mascons, which are detected on the Moon, Mars, and Mercury, as a new probe of the thermal history of these planets.

The model of Melosh *et al.* implies that as a planet cools, mascons may no longer form. When is it no longer possible to form a mascon? Is the mascon epoch different on Mars and Mercury? Mascons on Mars have a less well-developed low-density annulus than on the Moon (*10*). Is this an effect of the planet's size and surface modification processes on Mars? Melosh *et al.* lay the foundation for future work that will address these questions. As both the cratering and relaxation processes depend on the length scale of the mascon and on the acceleration of gravity, it may be possible to use the size of basins that produce mascons as a probe for strength stratification in the outer hundreds of kilometers of a planet in the distant past when these basins formed. It may also be possible to determine whether mascons could have formed in the larger and more active planets, such as Venus and Earth.

References

1. P. M. Muller, W. L. Sjogren, *Science* **161**, 680 (1968).
2. S. C. Solomon, J. W. Head, *Rev. Geophys.* **18**, 107 (1980).
3. G. A. Neumann, M. T. Zuber, D. E. Smith, F. G. Lemoine, *J. Geophys. Res.* **101**, 16841 (1996).
4. J. C. Andrews-Hanna, *Icarus* **222**, 159 (2013).
5. H. J. Melosh *et al.*, *Science* **340**, 1552 (2013); 10.1126/science.1235768.
6. M. A. Wieczorek, R. J. Phillips, *Icarus* **139**, 246 (1999).
7. L. G. J. Montesi, M. T. Zuber, *J. Geophys. Res.* **108**, 5048 (2003).
8. F. Nimmo, T. R. Watters, *Geophys. Res. Lett.* **31**, L02701 (2004).
9. S. C. Solomon *et al.*, *Science* **307**, 1214 (2005).
10. G. A. Neumann *et al.*, *J. Geophys. Res.* **109**, E08002 (2004).

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