

## RESEARCH ARTICLE SUMMARY

## MARTIAN GEOLOGY

# Deposition, exhumation, and paleoclimate of an ancient lake deposit, Gale crater, Mars

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**INTRODUCTION:** Remote observational data suggest that large bodies of standing water existed on the surface of Mars in its early history. This would have required a much wetter climate than that of the present, implying greater availability of water on a global basis and enhanced potential for global habitability. However, based on assumptions of a vast water inventory and models of atmospheric erosion, theoretical studies suggest a climate that was wetter but not by enough to sustain large lakes, even in depressions such as impact craters.

**RATIONALE:** The Mars Science Laboratory mission's rover, Curiosity, provides the capability to test hypotheses about Mars's past climate. The focus of the mission is the exploration of a ~5-km-high mountain, Aeolis Mons (informally known as Mount Sharp), located near the center of the ~140-km-wide Gale impact crater. Mount Sharp is underlain by hundreds of meters of sedimentary rock strata deposited ~3.6 billion to 3.2 billion years ago. These sediments accumulated in aqueous environments, recording the history of Mars's ancient climate. Because of Curiosity's ability to study these strata where they are exposed near the base of Mount Sharp, we can directly test the hypothesis that large impact craters were capable of accumulating

and storing water as lakes for substantial periods of time.

**RESULTS:** Over the course of 2 years, Curiosity studied dozens of outcrops distributed along a ~9-km transect that also rose ~75 m in elevation. Image data were used to measure the geometry and grain sizes of strata and to survey the textures associated



**Inclined strata in the foreground dip southward toward Mount Sharp and represent ancient delta deposits.** These deposits transition into strata in the mid-field that were deposited in ancient lakes. The buttes and mesas in the background contain younger deposits that overlie and postdate the lake deposits beneath Mount Sharp. The outcrop in the foreground is about 6 m wide, and the buttes and mesas in the background are hundreds of meters wide and tens of meters high. The image has been white-balanced. [Credit: NASA/Caltech/JPL/MSSS]

with sediment deposition and diagenesis. Erosion of Gale's northern crater wall and rim generated gravel and sand that were transported southward in shallow streams. Over time, these stream deposits advanced toward the crater interior, transitioning downstream into finer-grained (sand-sized), southward-advancing delta deposits. These deltas marked the boundary of an ancient lake where the finest (mud-sized) sediments accumulated, infilling both the crater and its internal lake basin. After

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infilling of the crater, the sedimentary deposits in Gale crater were exhumed, probably by wind-driven erosion, creating Mount Sharp. The ancient stream and lake deposits are erosional remnants of superimposed depositional sequences that once extended at least 75 m, and perhaps several hundreds of meters, above the current elevation of the crater floor. Although the modern landscape dips northward away from Mount Sharp, the ancient sedimentary deposits were laid down along a profile that projected southward beneath Mount Sharp and indicate that a basin once existed where today there is a mountain.

**CONCLUSION:** Our observations suggest that individual lakes were stable on the ancient surface of Mars for 100 to 10,000 years, a minimum duration when each lake was stable both thermally (as liquid water) and in terms of mass balance (with inputs effectively matching evaporation and loss of water to colder regions). We estimate that the stratigraphy traversed thus far by Curiosity would have required 10,000 to 10,000,000 years to accumulate, and even longer if overlying strata are included. Though individual lakes may have come and gone, they were probably linked in time through a common groundwater table. Over the long term, this water table must have risen at least tens of meters to enable accumulation of the delta and lake deposits observed by Curiosity in Gale crater. ■

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## RESEARCH ARTICLE SUMMARY

## STRUCTURAL BIOLOGY

## Structure and flexibility of the endosomal Vps34 complex reveals the basis of its function on membranes

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**INTRODUCTION:** The lipid kinase Vps34/PIK3C3 phosphorylates phosphatidylinositol to yield phosphatidylinositol 3-phosphate (PI3P). Vps34 is important for processes that sort cargo to lysosomes, including phagocytosis, endocytic traffic, autophagy, and cytosol-to-vacuole transport. In mammalian cells, the enzyme also has roles in cytokinesis, signaling, recycling, and lysosomal tubulation.

Vps34 is present in multiple complexes. Complex I functions in autophagy and contains Vps34, Vps15 (p150/PIK3R4 in mammals), Vps30/Atg6 (Beclin 1), and Atg14 (ATG14L). Complex II takes part in endocytic sorting (as well as autophagy and cytokinesis in mamma-

lian cells) and contains the same subunits as complex I, except that it has Vps38 (UVRAG) instead of Atg14. These complexes are differentially regulated in stress responses. In autophagy, PI3P emerges on small tubular or vesicular structures associated with nascent autophagosomes.

**RATIONALE:** One of the most compelling questions is how the Vps34-containing complexes are organized and to what extent their intrinsic properties contribute to their differential activities in cells. To understand the mechanisms by which these complexes impart differential activities to Vps34, we sought to determine the structure of com-

plex II and to characterize activities of Vps34 complexes on small and large vesicles. Because the complex resisted crystallization attempts, we screened 15 different nanobodies against the complex, and one of them enabled crystallization.

**RESULTS:** We obtained a 4.4 Å crystal structure of yeast complex II. The structure has a Y-shaped organization with the Vps15 and Vps34 subunits intertwining in one arm so that the Vps15 kinase domain interacts with

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the lipid-binding region of the Vps34 kinase domain. The other arm has a parallel Vps30/Vps38 heterodimer. This indicates that the complex might assemble by Vps15/Vps34

associating with Vps30/Vps38. This assembly path is consistent with *in vitro* reconstitution of complex II and suggests how the abundance of various Vps34-containing complexes might be dynamically controlled. The Vps34 C2 domain is the keystone to the organization of the complexes, and several structural elaborations of the domain that facilitate its interaction with all complex II subunits are essential to the cellular role of Vps34.

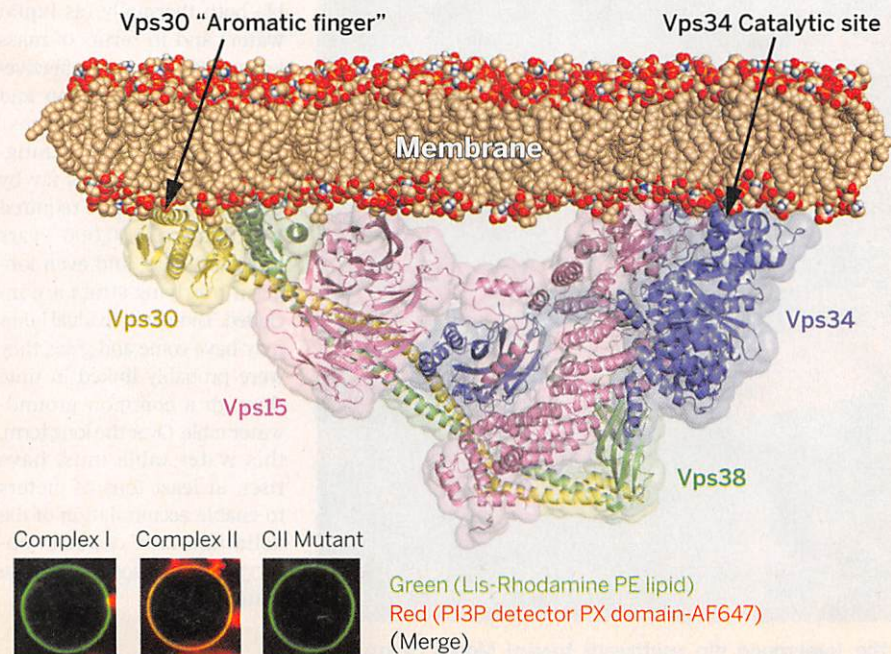
We used hydrogen-deuterium exchange mass spectrometry (HDX-MS) to identify localized changes in all four complex II subunits upon membrane binding. We identified a loop in Vps30 (referred to as the “aromatic finger”) that interacts directly with lipid membranes. Our assays showed that complexes I and II had similar activities on small vesicles (100 nm). In contrast, only complex II was active on giant unilamellar vesicles (GUVs) (2 to 20 μm). This activity was completely abolished by mutation of the aromatic finger.

**CONCLUSION:** The structure, HDX-MS, and functional data allowed us to devise a model of how Vps34 complexes adapt to membranes. The tips of both arms of complex II work together on membranes. The Vps30 aromatic finger in one arm is important for the efficient catalytic activity of the other arm. The conformational changes that we detected may allow the arms to open to accommodate low-curvature membranes such as GUVs and endosomes.

Most of the interactions observed in the complex II structure are likely to be detected in complex I as well. The restriction of complex I activity in autophagy to membrane structures smaller than 100 nm may be related to the inactivity of complex I on GUVs *in vitro*. ■

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**Structure of complex II and its activity on GUVs.** In the Y-shaped complex II, the Vps30/Vps38 pair in one arm brackets the Vps15/Vps34 pair in the other arm. Tips of both arms bind membranes. Only wild-type complex II forms PI3P on GUVs; in contrast, complex I and the complex II aromatic finger mutant are inactive. PI3P is detected by a sensor protein (red) binding to GUVs (green). Both complexes I and II have similar activities on small vesicles.