Introduction: Significant new chemical, geological, and computational evidence increasingly supports the hypothesis that life originated in hot spring fields on land, rather than at deep-sea hydrothermal vents. This has profound implications for Astrobiology and the search for life beyond Earth, not only for site selection on a planet, but also which of the planetary bodies to investigate. Herein we provide a broad framework of observations, a conceptual model, and implications for an origin of life (OoL) on land.

Observations: 1) Surface pools would have been able to concentrate in-fall from meteoritic sources and interplanetary dust particles, which were many times more voluminous during earliest Earth history [1] and contain abundant key building blocks for life including fatty acids, nucleobases, and amino acids [2-4].

2) Terrestrial hot springs have the capacity to undergo wet-dry cycling – in some cases many times per day (e.g., Yellowstone’s Old Faithful) – both at pool margins on the surface and in fractures in the near subsurface where prebiotic reactions would be shielded from harsh UV radiation. Wet-dry cycling has been shown to be critical in overcoming “The Water Problem”, whereby most of the important prebiotic organic reactions require a form of dehydration (condensation reactions, in which water is a leaving group) to form long-chain organic polymers (e.g., polysaccharides, oligonucleotides, and polypeptides) from their simple building blocks (e.g., amino acids) [5-7].

3) Hot spring pools, which contain a mixture of meteoric water and condensates of magmatic vapors, can be enriched in phosphorus, ammonia and organic compounds and produce a range of temperatures and pH, including mildly acidic pools that have been shown in the laboratory and at field sites to support the formation of membranous compartments or protocells [8-11]. Such protocells are able to encapsulate organic polymers and subject them to combinatorial selection through wetting-drying cycles that drive ever-increasing complexity and emergence of biological functions [12,13]. Freshwater is important because microorganisms from all three branches of life contain an internal cytoplasm with K+/Na+ ratios very different from seawater, or the possible compositions of ancient seawater, but similar to freshwater. Saltwater presents a barrier to the formation of protocells [14].

4) Hot spring pools can, and do, concentrate a variety of prebiotically important elements, including not only H, N, O, P, and C, but also Fe, S, and P, as well as B, Zn, and Mn [15,16].

5) Hydrothermal fields on land receive energy from three main sources: the hot spring system, dehydration energy, and UV light, the latter shown recently to support critical prebiotic reactions, including a pathway to activated nucleotides [17,18]. Another source is abiotic photosynthesis at ZnS and TiO2 crystals [19], both found in an ancient Pilbara hot spring analogue site [20,21].

6) Perhaps most important for an OoL scenario is the extreme complexity offered by terrestrial hydrothermal fields, which can consist of a hundred or more pools with widely ranging chemistry and temperatures. In addition, pools include not only the water-rock interactions that deep-sea vents have, but also water-air/volcanic gas, and air/volcanic gas-rock interactions. Pools also have the advantage of being able to exchange contents with other pools through flows, splashing, wind, and submarine plumbing networks that open and close on short geological timescales due to variable fluid/gas pressure and mineralization. Indeed, hot spring fields constitute a natural system for combinatorial or “messy” chemistry and support serial enrichment capable of creating a continuous supply of structures, building blocks, and energy sources to drive prebiotic processes through cycles of selection. Terrestrial pools are concentrating environments – through drying and evaporation – that permit many cycles of complex chemical reactions.

7) The “sweet spot” for supramolecular (e.g., non-enzymatic RNA duplex formation) assembly is ca. 10–70°C. This is because formation temperatures need to be high enough for molecules to “search” their conformation space (become distorted). Too cold and the lack of activation energy makes it doubtful that any “function” would occur between molecules – let alone generate life. Too hot and directional intermolecular forces are weakened and associations are too short for any chemistry useful for prebiotic selection to take place.
Conceptual Model: Testing of some of the above properties both in the laboratory and in the field has led to the publication of a new model for biogenesis in anoxic hydrothermal fields[11,13,15,22] (Fig. 1).

Figure 1. The Hot Spring Hypothesis for an origin of life, illustrating how organic compounds synthesize in space (1) and accumulate (2) within interconnected hydrothermal field pools (3). These organics are then delivered to a cycling pool where protocells undergo selection toward an origin of life (4). This earliest life is then distributed along an adaptation pathway into ever more extreme environments such as lacustrine (5), salty estuarine (6), and tidal marine (7) settings[13].

Implications: From an astrobiological perspective, the consideration of an OoL in terrestrial hot springs is important for two reasons. First, it can provide focused exploration strategies for planetary bodies where this combination of ingredients is known to have, or may have, occurred. Second, hot springs typically deposit opaline silica, providing an easily recognizable target in the search for evidence of life. Critically, hot springs are important not only as hosts of life, but their deposits can be preservers of biosignatures over billions of years[21,23-25]. Entombment of microbial mats and biofilms living on opaline silica deposits in and around hot springs results in the formation and preservation of numerous microbial biosignatures that include macro-to-microscale fabrics and structures, as well as organic and inorganic chemical traces of life[26,27]. Indeed, opaline silica is the most important primary mineraloid responsible for preserving morphologically and chemically identifiable traces of life on early Earth and is the most common host lithology – by a factor of 10:1 - of the most ancient traces of life in both the Pilbara (Australia) and Kaapvaal (South Africa) cratons[28,29].

Importantly, hot springs could truly be the "first and last outpost" for life on Mars, or any habitable world that becomes uninhabitable at its surface through loss of atmosphere, desiccation and irradiation. Life, if it emerged on Mars, would have had to retreat to refuges in the saline, deeper biosphere. The plumbing of a hydrothermal system could access that refuge and might carry such life with it through a temporary effusion of water up to a surface hot spring, where it may have temporary viability at this last surface outpost.

Robust evidence for hot spring deposits has already been identified on Mars by the Spirit rover adjacent to "Home Plate" in the Columbia Hills[28,29], including evidence for potential biosignatures[26]. Other candidate hot spring deposits have been observed from orbit, including mounds on the flanks of a volcanic cone in Nili Patera[30]. The combination of high potential for habitability and biosignature preservation of silica-depositing hot spring systems make them attractive astrobiology targets for future missions to Mars.