western ends than at the eastern. It has been assumed, as normal, that these wadis flowed eastward toward the Gulf. Were the notches, shaped like gigantic *V*'s, cut at the western ends of these canyons the results of normal stream erosion cutting into a dip slope that dipped downstream? Or did the streams originate in Tertiary times as west-flowing rivers, when the Afro-Arabian shield had not been uplifted?

In conclusion, the desert geomorphologist today finds that the desert is susceptible to systemic land-form analysis. Every land form in the desert has significance, if we can but determine what it means. Desert geomorphologists of the future, many of whom may come from the Middle East, will discover that there are still geomorphic frontiers in the Arabian deserts (*24*).

References and Notes

1. *Nafud* is the Arabic word for a large sandy desert, used mainly in the Najd.
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3. See map No. I-270-B-1 of the Arabian Peninsula (1:2,000,000) in *Miscellaneous Geological Investigations*, published (1958) by the U.S. Geological Survey and the Arabian American Oil Co., under the joint sponsorship of the Kingdom of Saudi Arabia and the U.S. Department of State, and maps Nos. I-213-B and I-214-B (1:500,000) in the same series (1959).
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24. This article is published by permission of the Arabian American Oil Co. General statements on climate and winds are derived from the company's meteorological records on file in Dhahran and from personal observation. Grateful acknowledgment is made to my colleagues, particularly G. P. Crombie, E. L. Elberg, Jr., L. F. Ramirez, and N. M. Layne, for many valuable discussions; to O. A. Seager, for support of this study; to I. A. Dugan for the sketch map; and to my wife, Esther A. Holm, for critical editing.

Specific Transport of Oxygen Through Hemoglobin Solutions

Why is this transport abolished when opposed by a slight back pressure of oxygen?

E. Hemmingsen and P. F. Scholander

It has recently been shown that under certain steady-state conditions oxygen moves several times faster through hemoglobin solutions than through water. In these experiments the solution was held in a Millipore membrane, above which was air at varying pressures and below which was moist vacuum. It was found that the nitrogen flux in all cases was strictly proportional to the diffusion pressure, but that the oxygen flux was enhanced. At air pressure of 1 atmosphere the oxygen-nitrogen ratio was almost double that of water, and at 1/12 atmosphere it was eight times higher than that of water. The following simple numerical relation prevailed in each case: Total oxygen flux = oxygen diffusion + a constant. Or, to express it more empirically: Total oxygen flux = nitrogen diffusion × 0.56 + a constant, where 0.56 is the O_2/N_2 ratio in the hemoglobin-free solution.

This was interpreted to mean that the oxygen flux proceeds via two separate routes—namely, a simple Fick's diffusion through the solution and a specific transport which is mediated by the hemoglobin. The latter is constant over a wide pressure range, increases with the concentration of the hemoglobin until the viscosity becomes excessive, and is abolished when the pigment is oxidized to methemoglobin. Suspensions of intact red cells and solutions of myoglobin show a similar effect (*1*).

These results were obtained by a gasometric technique which required that a near-vacuum be maintained below the membrane; it could not be used to study gas flow into a system containing oxygen of various tensions. In a muscle, zero or near-zero oxygen tension is relevant enough, but this would very rarely apply to the blood. The question therefore presented itself: What happens to oxygen transport through hemoglobin when the low pressure is elevated? In order to answer this question a new approach was needed, and it was highly desirable, also, to determine the state of oxygen saturation in the membrane at various pressures.

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Methods

Determination of gas flux against back pressure. A Millipore filter charged with hemoglobin solution was used to separate two large volumes of oxygen or nitrogen gas. When a pressure difference was applied, gas permeated the filter and the steady-state flux was determined.

Two 300-cm^3 gas chambers were moistened with a little water and interconnected through a capillary measuring device and a diffusion chamber (Fig. 1). The latter was divided into an upper and a lower half. The Millipore filter, resting on a rigid stainless steel screen, was clamped, airtight, between them. The graduated capillary, of 1- to 2-millimeter inside diameter, held a drop of kerosene for measuring the rate of gas flux. The drop could be reset at any time for repeated measurements by means of a three-way stopcock. Adequate sensitivity was obtained by keeping the gas volume between the drop and the membrane small (1 cubic centimeter). Change in the water content of the membrane by evaporation and condensation was the greatest source of error and was minimized by inserting a ring of wet filter paper in the lower diffusion compartment. The whole apparatus was immersed in a thermoregulated water bath.

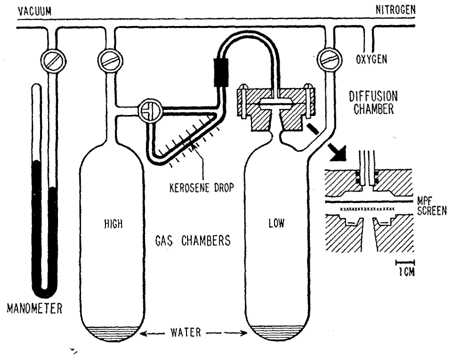

Fig. 1. Diffusion apparatus.

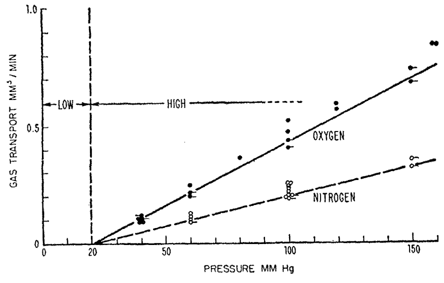

Fig. 2. Flux of oxygen and nitrogen through hemoglobin solution at an oxygen back pressure of 20 mm-Hg. Oxygen capacity, 20 to 21 vol percent. The marked points belong to sequences taken on two membranes. The other points are mostly single determinations from various membranes.

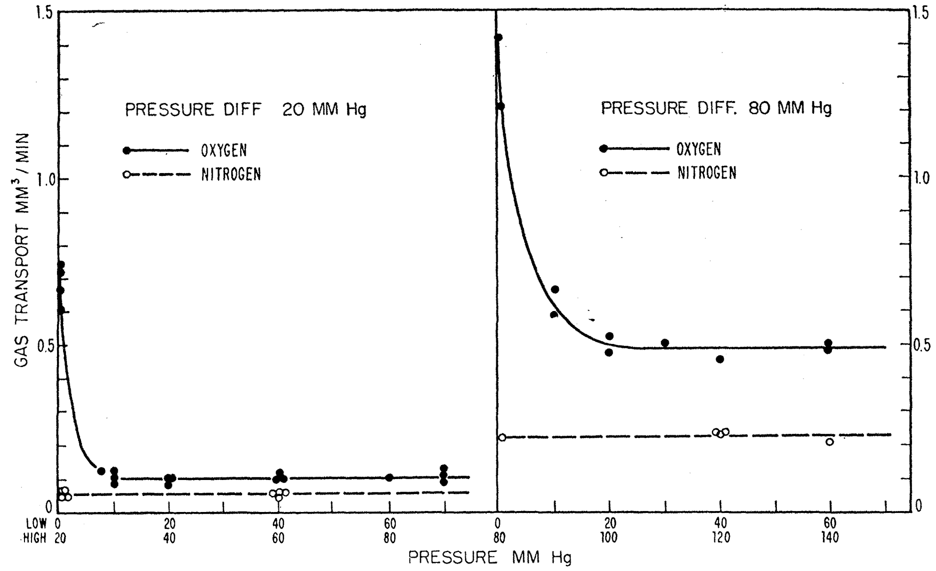

Fig. 3. Flux of oxygen and nitrogen through hemoglobin solution at constant pressure gradients but varying absolute pressures. Oxygen capacity of solutions, 20 to 21 vol percent. (Right) Two membranes at *p*H 7.2; (left) four membranes at *p*H 7.2, 7.3, 8.2, and 8.5, respectively.

Hemoglobin solutions were prepared from heparinized human blood, and the Millipore filter was charged with the solution, as previously described (*1*). With the membrane clamped, airtight, in the diffusion chamber, the system was evacuated and filled with purified oxygen (or nitrogen), evacuated again, and refilled. The desired pressure on the high and low sides of the membrane was obtained by means of the manometer. With the stopcock set as in Fig. 1, the rate of gas flux through the membrane was determined from the rate of movement of the kerosene drop. Final readings were taken when steady-state flux was reached. For each membrane the gas flow was determined at several different pressures, first with oxygen gas, then with nitrogen gas.

Determination of oxygen saturation in membrane. A membrane charged with hemoglobin solution was suspended in a flat plastic chamber which was kept moist with a strip of wet filter paper. The air spaces on each side of the membrane communicated with each other, and the air was maintained at various pressures. The state of oxygenation at each pressure was read on a reflectance spectrophotometer.

Two different series of experiments were performed in order to determine the effect of back pressure on the oxygen transport. In the first series the low pressure stayed constant at 20 mm-Hg, while the high pressure varied from 30 to 150 mm-Hg (Fig. 2). It may be seen that the transport of both nitrogen and oxygen proceeds exclusively by simple diffusion; that is, the rate is proportional to the gradient, and the oxygen moves nearly twice as fast as the nitrogen; there is no enhancement of the oxygen rate.

In the second series the total gas pressure varied while the pressure difference was maintained constant, either at 20 or at 80 mm-Hg (Fig. 3). It will be seen that the rate of *nitrogen* flux closely reflects the fourfold difference in gradient, and looking at each run separately, we find that the rates are constant all the way down to zero pressure; that is, the nitrogen moves by simple diffusion. In the case of *oxygen*, however, simple diffusion prevails only down to opposing oxygen pressure of 10 mm-Hg. Below this, the flux increases rapidly and reaches a maximum at zero back pressure; that is, the specific transport mediated by the hemoglobin is abolished when it is opposed by a slight back pressure of oxygen.

This blocking effect by oxygen is specific, for neither water-vapor pressure of 20 mm-Hg (moist vacuum) nor the addition of nitrogen to a pressure of 80 mm-Hg impedes the flux. The specific oxygen transport appears to be insensitive to temperature, for there was no clear difference in the oxygen-nitrogen ratio in runs made at 15° and 25°C. Likewise, there was no *p*H effect (compare Fig. 3, left), although such an effect becomes manifest at very low oxygen pressures (*1*).

The state of saturation of a membrane suspended in air at various pressures may be seen in Fig. 4. Full oxygenation occurs down to pressures of 30 to 25 mm-Hg, and one may therefore assume that our diffusion membranes were fully saturated, or nearly so, in the surface layer down to air pressure of ⅙ atmosphere. Similarly, it can be seen that the blocking pressure of 5 to 10 mm-Hg corresponds to less than half saturation of the lower surface. Evidently, therefore, a maximally accelerated oxygen transport requires full reduction pressure on one side of the membrane and full saturation pressure (or more) on the other.

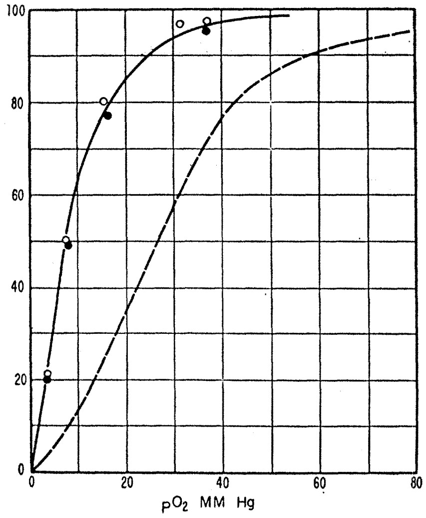

Fig. 4. Saturation of a membrane suspended in air at various pressures, measured by reflectance spectroscopy. (Left) Observed curve measured on two different membranes at 23°C, *p*H 7.3 and no carbon dioxide; (right) reference curve (37°C, *p*H 7.4, carbon-dioxide pressure, 40 mm-Hg) (*3*).

When the hemoglobin solution in the membrane was solidified by gelatine, the nitrogen diffusion remained unchanged but the specific oxygen transport was cut in half (*1*). This suggests that the oxygen transport is linked with the kinetic motion of the hemoglobin molecules. One concept would assume that a certain exchange of oxygen takes place from one hemoglobin molecule to the next when these collide. At the vacuum end of the chain there is no more than one oxygen molecule attached to the hemoglobin. When this molecule is lost to the vacuum, the deficit or "hole" is filled in from above; that is, the disturbance is transmitted through the entire chain in a rate-limited "bucket-brigade" fashion (*1*).

An alternative view would be that the transport is caused by oxyhemoglobin diffusing from one surface to the other. The porosity of the Millipore filter is much too fine for convection to take place, but hemoglobin readily diffuses into much finer structures, such as agar gels. Hence, some of the oxygenated molecules might carry oxygen downward and unload it to the vacuum, but if this is the case, an equal number of empty molecules would be moving upward, and one would expect these to receive oxygen from the loaded descending molecules. As in other countercurrent systems, such a cross exchange would strongly limit the net transfer. This concept is in line with the relatively low efficiency of our system. But neither of the proposed systems explains why a slight back pressure of oxygen should completely block further unloading.

What role does this hemoglobin transport system have in human beings? Presumably very little, if intact red cells are as sensitive to back pressure as is hemoglobin. If, however, the blocking pressure is related to degree of saturation rather than to absolute pressure, the transport might still be effective under tissue asphyxial conditions wherein the carbon dioxide tension and the presence of lactic acid have lessened the oxygen affinity (*2*).

References and Notes

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