Charles V. Paganelli
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Physiological Function in Special Environments

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Charles V. Paganelli
Leon E. Farhi
Department of Physiology
State University of New York at Buffalo
Buffalo, NY 14214
USA

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Preface

The numerous ways in which man and animals are affected by their physical environment, and the inborn and adaptive responses to change in the "milieu exterieur" have fascinated curious minds since the earliest days of recorded history. Development of the scientific method with its emphasis on evidence obtained through experimentation—perhaps best illustrated in this field by Paul Bert's encyclopedic work—allowed several generations of our predecessors to establish firmly some facts and reject erroneous beliefs, but it was only during the early 1940s that environmental physiology put on its seven-league boots.

In 1941, a young physiologist named Hermann Rahn was recruited by Wallace O. Fenn, then Chairman of the Department of Physiology at the University of Rochester, who was engaged in a study of the effects of altitude on human performance. The years that followed witnessed some of Hermann Rahn's early achievements not only in the area of altitude, but in other aspects of environmental physiology as well. In particular, he participated in the definitive studies of human adaptive mechanisms in arid climates which formed the basis of Edward Adolph's classic "Physiology of Man in the Desert" (Wiley/Interscience, NY 1947). During those golden years, environmental physiology flourished, and important discoveries were reported in a seemingly endless stream from many laboratories. From the perspective of more than 40 years, however, it seems fair to say that many, if not most, of the fundamental aspects of altitude and aviation physiology were described and analyzed by the Rochester triumvirate of Fenn, Rahn, and Otis from work carried out at the bench, in altitude chambers, and in field expeditions to remote places.

After 15 years in Rochester, during which Hermann Rahn rose to the rank of Vice Chairman of the Department, he assumed the leadership of the Department of Physiology at the University of Buffalo in 1956. Within a few years, he had gathered around him a team of younger investigators, many of whom had a demonstrated interest in diverse aspects of environmental physiology. Among the areas that were investigated over the following decade—with the support of such funding agencies as the National Science Foundation, the National Institutes of Health, the U.S. Navy Office of Naval Research, and the U.S. Air Force Office of Scientific Research—were the effects of altitude, diving, temperature, and gravity on human performance. Following the tradition started in

Rochester, research went hand-in-hand with training: scientists from the U.S. and around the world joined the Buffalo group for poriods ranging from several months to three years to participate in its work and "learn by doing."

Against this background, a symposium on environmental physiology was organized in Buffalo in October of 1985 to honor Hermann Rahn, and was the occasion for two other events celebrating his career in environmental physiology. By order of the Council of the University at Buffalo, the environmental physiology facility at our university was officially dedicated to Hermann Rahn, and named The Hermann Rahn Laboratory of Environmental Physiology. The second honor came from the U.S. Air Force in the form of the Meritorius Civilian Service Award, presented to him by Dr. Billy Welch, Chief Scientist, Human Systems Division, Brooks Air Force Base, at the symposium banquet.

The symposium itself took place on October 11 and 12, 1985 as a satellite of the American Physiological Society's Fall Meeting in Niagara Falls, and brought together an international group of 25 participants from the United States, Japan, West Germany, France, Israel, and Switzerland. The chapters in this volume were presented at that symposium; they cover a wide range of topics in environmental physiology, grouped into four general categories: Adaptation to Altitude; Diving and Exposure to Elevated Pressure; Exposure to Altered G-Force; and Comparative Physiology. In addition, Dr. Ewald Weibel, Professor of Anatomy and Director of the Anatomisches Institut, Universität Bern, provided an introductory chapter entitled "Fried Eggs on a Flying Saucer: Exploring the Pathway for Oxygen and Its Environment," originally an imaginative and beautifully illustrated lecture given at the symposium banquet, and intended, in the author's words, as a "surrealistic extension" of certain aspects of Hermann Rahn's many careers in physiology.

The present volume can obviously make no claim to all-inclusiveness. The field of environmental physiology is much too large to have been encompassed in a meeting lasting two days, as witness the many monographs and voluminous literature on the subject. The American Physiological Society's treatment of the topic in its *Handbook of Physiology* series alone occupies two volumes (one issued in 1964 and the second in 1977) and over 1,600 pages. Our selection of topics from a wealth of choices was dictated primarily by the fields of endeavor in which Hermann Rahn has made important, and in many cases, definitive, contributions. (Even so, we could not include temperature regulation for lack of time.)

We were aided in organizing the symposium and in our editorial work on the manuscripts by the Chairmen of the four sessions of the Symposium: Dr. S. Marsh Tenney, Nathan Smith Professor Emeritus of Physiology, Dartmouth Medical School (Altitude), Dr. Tetsuro Yokoyama, Professor of Medicine, Keio University School of Medicine,

Tokyo (Diving and Elevated Pressure); Dr. Arthur H. Smith, Professor Emeritus of Animal Physiology, University of California/Davis (G-Forces); and Dr. Claude Lenfant, Director, National Heart, Lung & Blood Institute, National Institutes of Health (Comparative Physiology). We wish to express to them our most sincere thanks for their efforts, without which the symposium could not have come to fruition. We should also like gratefully to acknowledge the financial support provided by the School of Medicine & Biomedical Sciences, University at Buffalo; by the American Physiological Society; by the Conferences in the Disciplines Program of the Graduate School, University at Buffalo; and by the Department of Physiology, University at Buffalo. Our warm thanks are also due to Mrs. Willie Brownie and Mrs. Julie Maciejewski who provided expert organizing and secretarial help, to Mr. Donald E. Watkins, of the Educational Communications Center, University at Buffalo, for his elegant design of the symposium logo which appears on the cover of this volume, and to the editorial and production staff of Springer-Verlag, New York, for patient assistance in bringing this book manuscript to publication. We particularly wish to express sincere gratitude to our colleagues in the Physiology Department at Buffalo for their help and encouragement in arranging the many details attendant on the symposium, and for their enthusiastic participation in the scientific sessions.

Finally, to Hermann Rahn, for his guidance and inspiration, we dedicate this volume with our admiration and thanks.

Charles Paganelli
Leon Farhi
Buffalo, New York
February 24, 1989

Contributors

Amos Ar
Department of Zoology, George S. Wise Faculty of Life Sciences, Tel Aviv University, Tel Aviv, Ramat Aviv 69978, Israel

R.R. Burton
Crew Technology Division, USAF School of Aerospace Medicine, Brooks, AFB, Texas 78235-5301, USA

P. Cerretelli
Department of Physiology, Centre Médical Universitaire, 1, rue Michel-Servet, 1211 Genève 4, Switzerland

Pierre Dejours
Laboratoire d'Etude des Regulations Physiologiques, associé à l'Université Louis Pasteur, CNRS, 23 rue Becquerel, 67087 Strasbourg, France

Jerome A. Dempsey
John Rankin Laboratory of Pulmonary Medicine, Department of Preventive Medicine, University of Wisconsin Medical School, Madison, Wisconsin 53706, USA

P.E. di Prampero
Department of Physiology, Centre Médical Universitaire, 1, rue Michel-Servet, 1211 Genève 4, Switzerland

Konrad Falke
Department of Anesthesia, University of Berlin, D 1000 Berlin 19, West Germany

LEON E. FARHI
Department of Physiology, State University of New York at Buffalo, Buffalo, New York 14214, USA

J. FASULES
Cardiovascular Pulmonary Research Laboratory B-133, University of Colorado Health Sciences Center, 4200 E. 9th Avenue, Denver, Colorado 80262, USA

H.T. HAMMEL
Department of Physiology, Meyers Hall, Indiana University, Bloomington, Indiana 47405, USA

ROGER D. HILL
Department of Anesthesia, Massachusetts General Hospital, Boston, Massachusetts 02114, USA

PETER W. HOCHACHKA
Department of Zoology, University of British Columbia, Vancouver, British Columbia, Canada V6T 2A9

D.C. HOFFMAN
Department of Physics and Astronomy, University of Hawaii, Honolulu, Hawaii 96822, USA

SUK KI HONG
Department of Physiology, State University of New York at Buffalo, Buffalo, New York 14214, USA

H. HOWALD
Department of Physiology, Centre Médical Universitaire, 1, rue Michel-Servet, 1211 Genève 4, Switzerland

PHILIP C. JOHNSON, JR.
NASA/Johnson Space Center, Biomedical Laboratories Branch, Mail Code SD4, Houston, Texas 77058, USA

SUKHAMAY LAHIRI
Department of Physiology, University of Pennsylvania School of Medicine, Philadelphia, Pennsylvania 19104, USA

CAROLYN S. LEACH
NASA/Johnson Space Center, Biomedical Laboratories Branch, Mail Code SD4, Houston, Texas 77058, USA

Graham C. Liggins
National Women's Hospital, Postgraduate School of Obstetrics and Gynecology, Auckland 3, New Zealand

Y. Ohta
Department of Medicine, School of Medicine, Tokai University, Bohseidai, Isehara, Japan 259-11

Charles V. Paganelli
Department of Physiology, State University of New York at Buffalo, Buffalo, New York 14214, USA

Johannes Piiper
Abteilung Physiologie, Max-Planck-Institut für experimentelle Medizin, Hermann-Rein-Str. 3, 3400 Göttingen, West Germany

Jesper Qvist
Herlev Hospital, Department of Anesthesia, Copenhagen, DK 2730 Herlev, Denmark

Hermann Rahn
Department of Physiology, State University of New York at Buffalo, Buffalo, New York 14214, USA

J.T. Reeves
Cardiovascular Pulmonary Research Laboratory B-133, University of Colorado Health Sciences Center, 4200 E. 9th Avenue, Denver, Colorado 80262, USA

Robert C. Schneider
Department of Anesthesia, Massachusetts General Hospital, Boston, Massachusetts 02114, USA

Curtis A. Smith
John Rankin Laboratory of Pulmonary Medicine, Department of Preventive Medicine, University of Wisconsin Medical School, Madison, Wisconsin 53706, USA

K.R. Stenmark
Cardiovascular Pulmonary Research Laboratory B-133, University of Colorado Health Sciences Center, 4200 E. 9th Avenue, Denver, Colorado 80262, USA

A. Tucker
Department of Physiology, Colorado State University, Fort Collins, Colorado 80523, USA

Hugh D. Van Liew
Department of Physiology, State University of New York at Buffalo, Buffalo, New York 14214, USA

Ewald R. Weibel
University of Bern, Buhlstr. 26, Postfach 139, Bern 9, Switzerland

D.E. Yount
Department of Physics and Astronomy, University of Hawaii, Honolulu, Hawaii 96822, USA

David Zacks
Department of Zoology, George S. Wise Faculty of Life Sciences, Tel Aviv University, Tel Aviv, Ramat Aviv 69978, Israel

Warren M. Zapol
Department of Anesthesia, Massachusetts General Hospital, Boston, Massachusetts 02114, USA

Chairpersons of the Sessions

Satellite Symposium on Environmental Physiology, Buffalo, October 10–12, 1985

I. Physiology of Adaptation to Altitude
Stephen M. Tenney
Department of Physiology
Dartmouth Medical School
Hanover, New Hampshire 03756, USA

II. Physiology of Diving and Exposure to Elevated Pressure
Tetsuro Yokoyama
Department of Medicine
Keio University School of Medicine
35 Shinanomachi, Shinjuku-ku
Tokyo 160, Japan

III. Physiology of Exposure to Altered *G*-Force
Arthur H. Smith
Department of Animal Physiology
University of California, Davis
Davis, California 95616, USA

IV. Comparative Physiology
Claude Lenfant
National Heart, Lung and Blood Institute
NIH Bldg 31
Bethesda, Maryland 20892, USA

Fried Eggs on a Flying Saucer: Exploring the Pathway for Oxygen and Its Environment

Banquet speech at the Symposium on Environmental Physiology, dedicated to Hermann Rahn

EWALD R. WEIBEL

"Romance, relevance, and diving" is the title Hermann Rahn chose for his acceptance speech for the Behnke Award. "Fried eggs on a flying saucer"—this title also has to do with relevance and romance as they may relate to Hermann Rahn's vast oeuvre, which began with as relevant topics as the anatomical study of the chick pituitary, but then went on to look at rattlesnakes, water dogs, diving amas, lungfish, bird embryos, and all aspects of the environment from high to low pressure and weightlessness. But I noticed some missing points. And so I thought I should attempt something like a surrealistic extension of this oeuvre, primarily by considering some of the enigmatic beauty that nature has associated with several of its aspects.

In my view Hermann Rahn is a true naturalist who knows no limit to his inquisitiveness. As we all know, he is a bird watcher, an avid observer of everything that flies around—and I would certainly not be surprised if he were one of the few who have ever seen a flying saucer over the horizon. And I would not be surprised either if he were to cherish the romantic idea of boarding one of these flying objects that know no limit for pervading the environment or even diving into the universe, because they must be fascinating vantage points from where to take a new look at our world, a look beyond diving or flying in weightlessness.

For a bird watcher it is natural that he should be concerned with their eggs, and we all know of Hermann Rahn's extended inquiries into how eggs breathe (Rahn et al. 1979). But there is one extension of his work on eggs which is of evident relevance for practical life. This is the fact that small birds have small eggs, and big birds big eggs. It is evident that a fried ostrich egg would be much more spectacular than a fried hummingbird egg. But there is one problem which Hermann Rahn has realized, and this is that big eggs have a thicker shell, more difficult to crack. So he measured the yield point of the shell of eggs of different mass, i.e., the minimum force F required to break the shell (Ar et al. 1979). The significant result is that big eggs offer a great advantage. Since the minimum force *F* increases with egg mass to the power 0.9, the relative force required to crack an egg—i.e., the force required per mass of egg that falls into the frying pan—this force is twice as large in a hummingbird egg as compared with an ostrich egg.

The first message is clear, particularly if one were to prepare for an expedition on a flying saucer: big eggs are more economical than small ones.

The vantage point of an imaginary expedition on a flying saucer would in fact be significant for Hermann Rahn's approach as a naturalist, which is to be an observer of nature in all its aspects, to look keenly, inquisitively at every detail, and then to put it into perspective. Here began my problems in preparing for this talk: in trying to define his perspective. I thought it might be expressible in three-dimensional space—but no way. In this situation Hermann Rahn would say: no problem, just take the O_2-CO_2 diagram and everything becomes simple, because every point on it has a multidimensional perspective (Rahn and Fenn 1955). This device is indeed rather impressive, and I had wondered how anyone could invent it, until I realized that Hermann Rahn may have come up with the concept when watching birds. Specifically peacocks whose tail fan has an astonishing likeness to some of the curves derived with the O_2-CO_2 diagram (Fig. 1). Indeed we find that the eyes of the tail fan are distributed along well-defined curves, at the intersection of equiangular or logarithmic spirals, Bernoulli's spira mirabilis, the characteristic growth curve of the nautilus.

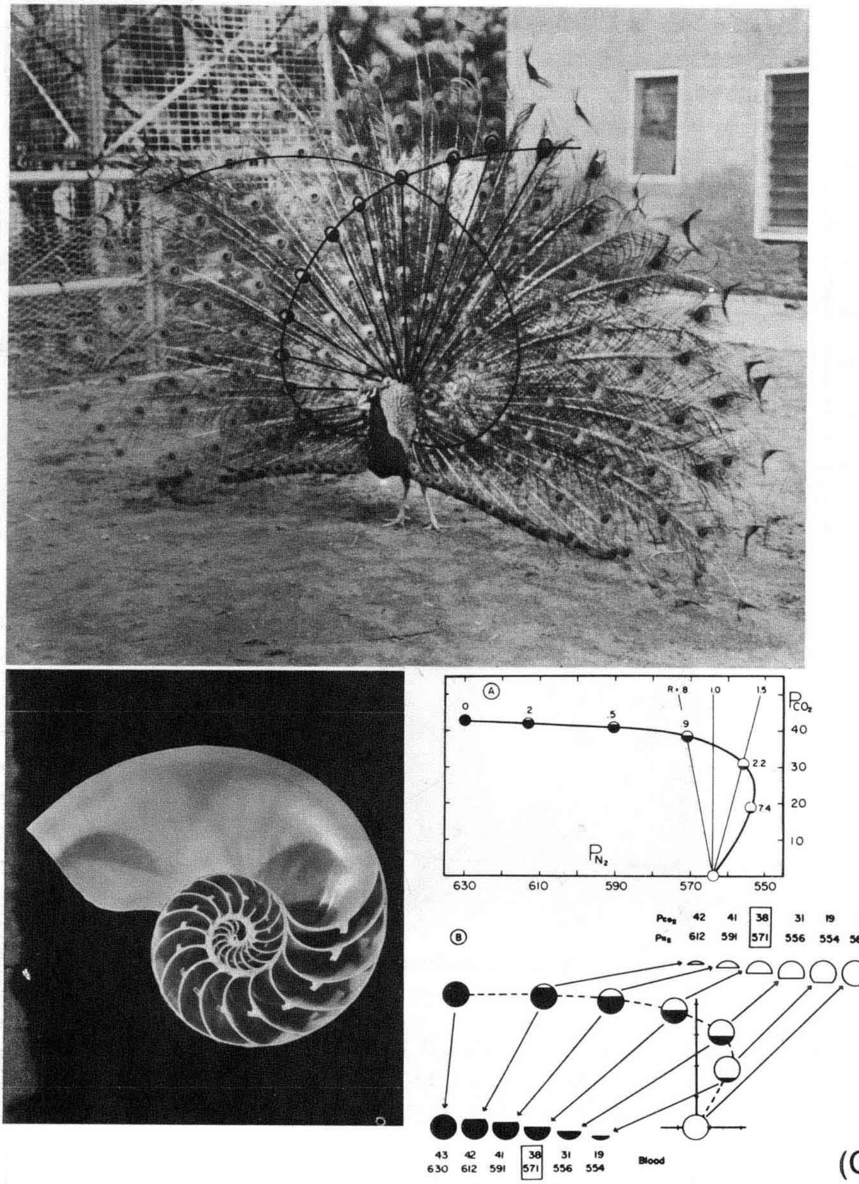
Beyond this aesthetic quality, the O_2-CO_2 diagram is also quite useful as it presents the pathway for O_2 from inspired air to the cells in a rather compact way. However, I must confess that I also find it rather boring, and perhaps misleadingly simple. It does away with too much of the intricate complexity, of the beauty of the system that makes it possible for the points to be so neatly arranged. What matters for me is what is between the points. This is what I would like to pull into the picture now, by sketching out the design of the respiratory system, following the pathway for O_2 from the lung to the mitochondria (Weibel 1981), and by considering how some of its design properties relate to its functional performance (Fig. 2).

The model on which we operate is closely related to the O_2-CO_2 diagram and to the concept of a PO_2 cascade as a driving force for O_2 flow (Fig. 3). The basic notions are these:

1. The rate at which O_2 must flow through the system is determined by the rate at which it is consumed in the mitochondria, primarily the mitochondria in muscle when we talk about high flow rates close to the limit of aerobic performance.
2. At each level of the system the flow rate is determined by a PO_2 difference as a driving force and by a conductance which is in part determined by design properties.

(A)

(B)



(C)

FIGURE 1. The eyes on a peacock tail fan (*a*) are located at the intersections of equiangular spirals, the characteristic growth curve of the nautilus (*b*). Gas tension curves of Rahn (*c*) for comparison (Used by permission of Hermann Rahn).

FIGURE 2. The respiratory system and a famous bird watcher.

3. The system is well designed if the conductances are matched to the functional flow requirements under limiting conditions of O_2 consumption. We have called this concept "symmorphosis." (Weibel and Taylor).

I would like to briefly discuss three levels: the lung, the mitochondria, and the capillaries in muscle (Fig. 4). Let me begin with the mitochondria, the sinks into which O_2 disappears in the process of oxidative phosphorylation. When looking at a large variety of animals, including trained and untrained humans, we observed that the total volume of mitochondria in muscle is directly proportional to VO_2 max. This suggests that it is the mitochondria that limit O_2 consumption and by that aerobic metabolism (Hoppeler and Lindstedt 1985). We have looked at this more closely.

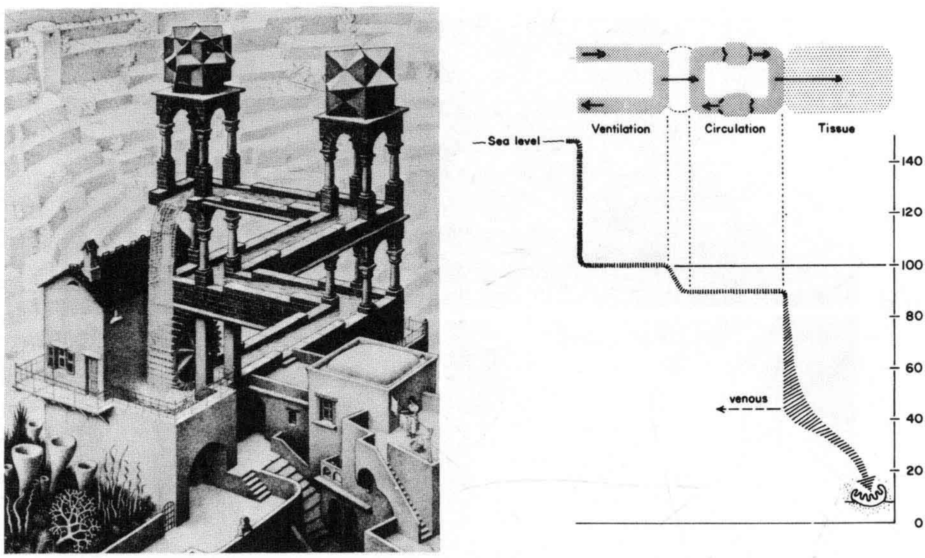


FIGURE 3. Hermann Rahn's PO_2 cascade (1962) (used by permission of Hermann Rahn) and M. C. Escher's miraculous Waterfall of 1961. © 1988 M. C. Escher Heirs/Cordon Art-Barn-Holland)

Aerobic metabolism, or rather oxidative phosphorylation, takes place in the inner membrane of the mitochondria (Fig. 4*d*), where a complex of rather densely arranged respiratory or energy-transducing enzymes entertains a flux of electrons within the membrane, coupled to a flux of protons across the membrane, which, in the end, makes ATP and uses O_2 at the cytochrome oxidase (Fig. 4*e*). By measuring enzyme densities in these mitochondria (Schwerzmann 1986), we have recently estimated that this system operates in vivo close to its maximal reaction rate, namely, at about 24 oxidations per second per cytochrome oxidase when muscles work at their maximal aerobic capacity. This is strong evidence that O_2 consumption is indeed limited by the amount of mitochondria that can perform oxidative phosphorylation. So at the last step of the respiratory system the flow of O_2 is determined by the size of the sink, or by the conductance at this level.

What about the next level, the delivery of O_2 to the cells which must be related to the capillaries (Fig. 4*c*), as we suspect since A. Krogh's pioneering work. Are capillaries matched to the O_2 needs of the cells? Apparently, because we find over a wide range of muscles (from cow locomotor muscles to the myocardium of the shrew) a constant volume ratio of mitochondria to capillary blood, namely 3 ml mitochondria per 1 ml blood. Let us look at what this means. By combining physiological with morphometrical measurements, Hans Hoppeler has estimated that

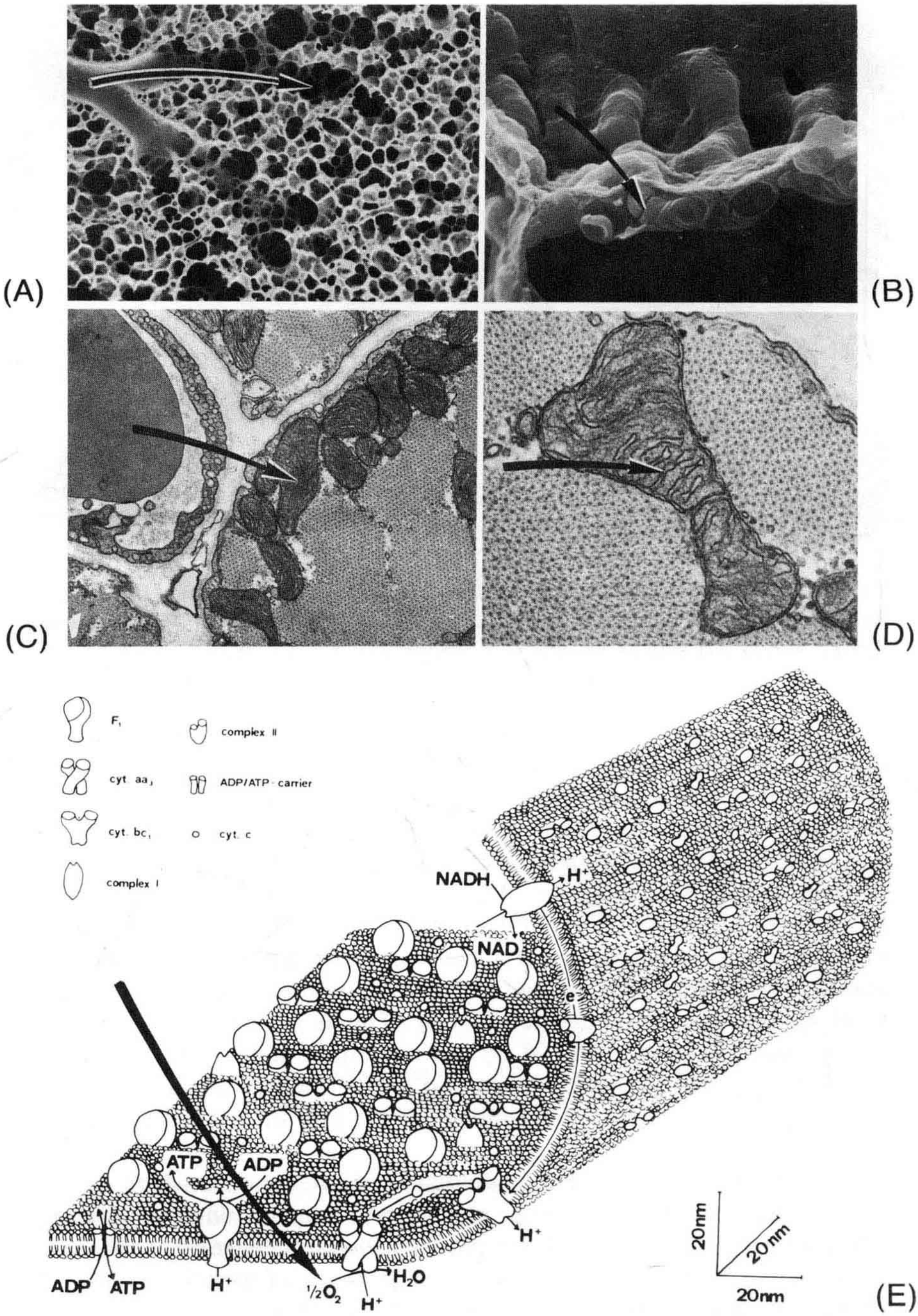


FIGURE 4. The pathway for oxygen (arrows) from the lung (*a*, *b*), through capillaries (*c*), to muscle mitochondria (*d*), where O_2 is consumed on the molecular complexes of the inner membrane (*e*).