Preface

With a surface area of 100 m^2 and a capacity of some 6 L, approximately 10% of which is exchanged during each of the15 breaths taken every minute, the lungs are the most likely portal for systemic intoxication by airborne pathogens and toxins. Pathogens are disease-producing microorganisms. Bacteria, mycoplasma, rickettsia, fungi and viruses are among the naturally occurring pathogens. Toxins are poisons produced through the metabolic activities of living organisms. They are organic chemical compounds such as proteins, polypeptides and alkaloids that come from a variety of biological sources.

In Chapter 1, Henderson and Salem discuss the relationships between the structure and historical development the atmosphere of and the presence of airborne microbial life. They address the questions of contributions from the atmosphere to the origin and evolution of microbial life and whether the atmosphere can be considered as the true habitat for airborne microorganisms. These are indeed relevant questions considering the diverse array of airborne microbes identified in collaborative research by the University of Colorado Denver and the North Carolina State University. The study reported more than 110 000 bacterial species and more than 55 000 fungal species in dust samples collected from 1200 homes representing locations in all 50 states. The average dust sample contained 4700 bacterial species and 1400 fungal species.[1] Some of these microbes could be carried on airborne dusts of terrestrial origin and/or in airborne mists of aquatic origin. At present, it is undecided if the atmosphere is a habitat for microbes or merely a conduit for their dispersal.

Airborne bacteria are responsible for diseases such as anthrax (*Bacillus anthracis*), diphtheria (*Corynebacterium*), legionellosis (*Legionella pneumophila*), meningitis (*Neisseria* species), pneumonia (*Mycoplasma pneumoniae*, *Streptococcus* species), tuberculosis (*Mycobacterium tuberculosis*) and

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whooping cough (*Bordetella pertussis*). Chickenpox (varicella zoster virus) and smallpox (variola major virus), influenza (influenza virus), measles (morbillivirus) and German measles (rubellavirus) and mumps (rubulavirus) are among the diseases of viral origin communicable by airborne transport. Psittacosis (*Chlamydia psittaci*), aspergillosis (*Aspergillus fumigatus*, *A. flavus*, *A. niger*), histoplasmosis (*Histoplasma capsulatum*) and coccidioidomycosis (*Coccidioides immitis*) are examples of infections in humans initiated by the inhalation of fungal spores and their deposition in the alveoli. In addition to infections with microbial pathogens, some of their airborne metabolic by products are toxic. Some examples of such toxins are aflatoxin, a hepatotoxin of fungal origin (*Aspergillus flavus*, *A. parasiticus*), botulinum toxin, a neurotoxin of bacterial origin (*Clostridium botulinum*) and ricin, a cellular toxin extracted from the caster oil bean (*Ricinus communis*).

The recent outbreak of measles demonstrates the importance of immunization in providing effective protection against this viral disease.[2] Measles is only one of the two dozen or so vaccine-preventable diseases. During the 225 years since Jenner "vaccinated" 8-year-old James Phipps with exudate taken from a cowpox lesion on the hand of dairy maid Sarah Nelms,[3] routine vaccination against smallpox has virtually eliminated this disease from human infection. However, Vora *et al.*[4] reported the infection of three unvaccinated Georgian dairy men with an orthopoxvirus as recently as 2013. In Chapter 2, Ibrahim and Meyer describe animal models, pathogenesis, vaccine and drug studies for smallpox and the other orthopoxviruses. Smallpox is a human disease. Each of the animal models was able to mimic some features of the human disease and collectively the mousepox, rabbitpox and monkeypox models contributed significantly to understanding the pathogenesis of the disease and to developing new generations of vaccines.

Recent media reports[5–7] on the unintentional shipment of live anthrax spores from the Dugway Proving Ground to as many a 68 external institutions on 22 May 2015 are reminders of the continuing need for planning, developing and implementing emergency response strategies. Hamilton *et al.*[8] have presented an analysis of post-attack strategies for mitigating risks associated with reoccupying areas contaminated with *Bacillus anthracis*. In Chapter 3, Falk and Eisenkraft evaluate the inhalation hazard and the dose–response relationships for anthrax, which is another vaccine-preventable disease. They focus on their relevance to risk analysis and response planning and on their relevance to the mitigation of biological terrorism and biological warfare attacks. The review by Shah *et al.* in Chapter 7 considers the aerodynamics of anthrax particles, their mechanisms of infection at the molecular level and the manifestations of infection at the clinical level, in addition to diagnosis and treatment of the inhalational, cutaneous, gastrointestinal and injectional forms of the disease. Timely and relevant considerations of anthrax protection, detection and decontamination are included in this chapter.

Shannon Guess Richardson[9] and Nicholas Helman[10] attempted to use "ricin letters" as tools for assassinating a sitting president and a rival suitor, respectively. Both were captured, tried, found guilty and incarcerated. The Bulgarian defector Gregori Markov is thought to have been assassinated with a ricin-injecting umbrella during the cold war.[11] Pincus *et al.*[12] have focused on the potential use of aerosolized ricin as a bioweapon for use against civilian and military personnel and they have reported on the clinical aspects of inhalation exposure to ricin. Henderson *et al.* present a detailed description of ricin toxicity at the molecular level in Chapter 5.

The Working Group on Civilian Biodefense[13] developed consensus-based recommendations for measures to be taken by medical personnel and public health officers in the event that botulinum neurotoxin was used as a biological weapon against a human population. The 23 members of the Working Group, representing academic, government and private institutions, were experts in public health, emergency management and clinical medicine. They concluded that an aerosol- or food-borne botulinum neurotoxin weapon would cause acute systemic, descending flaccid paralysis with bulbar palsies such as diplopia, dysarthria, dysphonia and dysphagia that would typically present 12–72 h after exposure. Effective response to a deliberate release of botulinum toxin would depend on timely clinical diagnosis, case reporting and epidemiological investigation. Persons potentially exposed to botulinum neurotoxin should be closely observed and those with signs of botulism would require prompt treatment with antitoxin and supportive care that would include assisted ventilation for weeks of months. The treatment with antitoxin should not be delayed by microbiological evaluation. Park and Simpson[14] reported that rats vaccinated with the heavy chain component of the botulinum neurotoxin were completely protected when exposed to doses up to several thousand times the LD_{50}. In Chapter 4, Adler and Franz review the consequences of exposure to botulinum neurotoxin by both the ingestion and inhalation routes. They cite the effectiveness of treatment with equine antitoxins in non-human primates exposed to botulinum neurotoxin by the inhalation route. Like Park and Simpson,[14] Adler and Franz stress the need for initiating treatment promptly.

The threat of bioterrorism and pandemics has highlighted the urgency for rapid and reliable bioaerosol detection.[15,16] Early detection of airborne pathogens and toxins is essential for reducing contagion and initiating protective measures. In Chapter 6, Santarpia identifies the compositions of ambient biological aerosols, discusses the roles of bacteria, viruses and fungi and reviews methods for their measurement. In Chapter 8, Trebše *et al.* review the chemical, physiological, biochemical and immunochemical principles serving as the basis of methods for the detection of airborne pathogens and toxins and the applications of these principles to their detection and measurement.

Several aspects of particle physics were considered by Polymenakou[17] in his review on bioaerosols. In Chapter 9, Corriveau discusses these aspects as they relate to the weaponization of biological agents. In Chapter 10, Kesavan *et al.* discuss the impacts of particle size, shape, density, surface area, mass and concentration on predicting the movements of bioaerosols.

In Chapter 11, Bona and Katz include these parameters in their discussion of the models for air filtration, and also identify some of the airborne pathogens and toxins, compare air filtration devices and describe some applications of respiratory protection devices.

Aerial dispersion of pathogens is a potential route for the spread of infection. King *et al.*[18] have combined computational fluid dynamics simulations of bioaerosol deposition with a probabilistic healthcare workers surface contact model to estimate pathogen accrual. In Chapter 12, McClellan *et al.* describe the Deposition And Response in the Respiratory Tract (DARRT) model, which accounts for variations in human response caused by differences in particle size, in particular, for coarse particles that may be present near an aerosol dissemination source and that may remain suspended long enough in an urban environment to expose large numbers of people. In Chapter 13, Reed *et al.* describe and discuss several reproducible exposure methods for producing standardized infections by inhaled viral and bacterial agents. In Chapter 14, Ingersoll and Williams present computer code for agent-based disease models in the mathematical programming language R allowing characterizations of the dynamics of infectious diseases in host communities.

The contents of these chapters are intended to provide information for the protection of human health from the harmful effects of airborne pathogens and toxins. Continued research and development will undoubtedly change some of these perspectives. This is especially true in the areas of detection and protection. Consequently, the work presented here is a starting point for further enhancement of the quality of life in all parts of Planet Earth.

Sidney A. Katz
Cherry Hill, NJ
Harry Salem
Edgewood, MD

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CHAPTER 1

The Atmosphere: Its Developmental History and Contributions to Microbial Evolution and Habitat[†]

TERRY J. HENDERSON*[a] AND HARRY SALEM[a]

[a]Research and Technology Directorate, US Army Edgewood Chemical
Biological Center, Aberdeen Proving Ground, MD 21010–5424, USA
*E-mail: terry.j.henderson.civ@mail.mil, harry.salem.civ@mail.mil

1.1 Introduction

Research efforts focused on the Earth's biota have been limited almost exclusively to land, soil and aquatic habitats; however, this focus is now beginning to change. There is a renewed and building interest in the ecology of living microorganisms found in the atmosphere. Hundreds of thousands of individual microorganisms can exist in a cubic meter of air,[1] which can represent hundreds of different taxa.[2,3] The atmosphere is one of our Planet's most intriguing habitats to investigate because extreme cold temperatures,

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[†] The opinions expressed in this chapter are the private views of the authors and are not to be construed as an official Department of the Army position unless so designated by other authorizing documents. This chapter has been approved for public release.

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hypobaria (low pressures), desiccation and ultraviolet (UV) irradiation make it more indicative of the surface conditions on Mars rather than anywhere else on Earth.[4] In a recent report,[5] the atmosphere was described as "one of the last frontiers of biological exploration on Earth."

The Planet's atmospheric biota, however, remains one of the most challenging to investigate, which has been reflected by the many shortcomings encountered throughout the history of aerobiology. In the past, aerobiological studies relied almost exclusively on culture-based analyses that neglected the vast majority of microbes present in air samples.[1,6,7] This is because only 0.1–10% of the total airborne microbial flora are able to grow in culture.[8–10] Airborne microorganisms can also become damaged or killed by desiccation, UV irradiation or the extreme low temperatures that occur in the atmosphere. Acquiring culture-independent microbiological data, on the other hand, can be difficult because the density of airborne microorganisms decreases with increasing altitude.[1,11] Large, or sometimes enormous, volumes of air must be collected and processed for detecting microorganisms with molecular detection assays and air-sampling systems must also be designed to prevent cell trauma and damage and sample contamination. To complicate matters, a modern, standard method for reading and scoring microorganisms in aerobiological samples does not exist, making the interpretation and intercomparison of results difficult.[12] Finally, studies of atmospheric residence times (the lifetime of particles aloft in the atmosphere) for microorganisms and their dispersal patterns rely on computer simulations based on theoretical mathematical models that are difficult to correlate with experimental data.[4,6,13] Such experimental design and engineering challenges explain why the upper atmosphere is one of the least explored biological environments on Earth, rivaling deep oceanic and subsurface environments.

Given the renewed interest in aerobiology and the inherent difficulties in aerobiological research, it should be of no surprise that the field is characterized by a remarkable lack of knowledge and a great deal of speculation. Some of the most important and fundamental questions regarding microorganisms in the atmosphere cannot be answered definitively and are active topics of debate. Undoubtedly, one of the more fundamental questions concerns the contributions of the atmosphere to the origin and evolution of microbial life. A complete account of this topic should include the evolutionary history of airborne microorganisms, the details of which have never been addressed to date. Another question central to aerobiology is whether the atmosphere can be considered a true habitat for airborne microorganisms. Several recent reports allude to the atmosphere as a habitat or ecosystem,[14] especially in the case of microorganisms,[6,15] but others argue that the debate is far from settled[4,16] and subscribe to the more traditional point of view that the atmosphere is merely a conduit for dispersing microbes to distant locations. Other important problems in aerobiology have somewhat vague and tenuous answers simply because they are difficult to answer by experimentation. For microorganisms in particular, the most fundamental of these concern deriving realistic values for atmospheric residence times[17] and understanding cosmopolitan dispersal by atmospheric transport (see, for example, Fröhlich-Nowoisky *et al.*,[18] Wilkinson *et al.*[13] or Smith *et al.*[19]). Atmospheric air is the primary medium for dispersing microorganisms across the globe and connecting all microbial habitats on the Earth's surface, but it is not known whether the atmosphere contains biogeographic regions similar to those found on the Planet's surface.[6,18] We discuss the most recent research focused on establishing more concrete answers to these questions and, when appropriate, present our own speculation. Because the developmental history of the atmosphere is intimately related to microbial evolution and because some understanding of atmospheric structure is necessary to discuss aerobiology in detail, we begin by outlining this history and the Earth's present-day atmosphere.

1.2 The Origin and Evolution of the Earth's Atmosphere

The processes by which the current atmosphere arose from earlier conditions are exceedingly complex; however, evidence related to these processes, although indirect, is abundant. Ancient sediments and rocks record the past changes in the atmospheric composition from chemical reactions within the crust, and also the evolutionary history of living systems. Several processes, including plate tectonics, weathering and photosynthesis, were internal to the Planet. However, extra-planetary processes such as the slowly and ever-increasing luminosity of the Sun over billions of years, gradual changes in the Earth's orbit over many tens of thousands of years and the rare but catastrophic impacts of giant meteorites and comets, have also played important roles. Collectively, these factors have forged three distinct atmospheres for the Earth: an initial, tremendously hot atmosphere composed principally of H_2 (hydrogen) and He (helium) gases, a second, rich in gaseous N_2 (nitrogen) and CO_2 (carbon dioxide), and today's atmosphere, rich in gaseous N_2 and O_2 (oxygen).

1.2.1 The Primary Atmosphere of the Earth

The oldest materials ever found in the Solar System occur in meteorites ~4.57 Ga (gigaannum or billion years ago) of age,[20] marking the starting point for the condensation of the first solids in our Solar System. At this time, Earth was tremendously hot and inhospitable due to collisions and compressions of matter during accretion (the growth of a massive object by gravitationally attracting more and more matter, typically gaseous matter), heat released from the formation of an early planetary core and the ubiquitous, constant decay of radioactive elements. The Planet's earliest surface was molten or a thin and unstable basaltic crust with constant volcanism. This was the birth of planet Earth and, as shown in Table 1.1, marked the start of geological time. Earth's atmosphere likely consisted of gases captured from the solar nebula (the gaseous cloud from which the Sun and planets are believed to have formed by condensation)[21–23] with H_2, by far the most abundant element in the Universe, as its principal component. Other atmospheric gases

Table 1.1 Geological time scale.

Eon	Era	Period	Millions of years before the present
Precambrian			4500–570
	Archean		4500–2500
		Hadean	4500–3900
		Early Archean	3900–2900
		Late Archean	2900–2500
	Proterozoic		2500–570
		Early Proterozoic	2500–1600
		Middle Proterozoic	1600–900
		Late Proterozoic	900–540
Phanerozoic			570–present
	Paleozoic		540–225
		Cambrian	540–500
		Ordovician	500–430
		Silurian	430–395
		Devonian	395–45
		Carboniferous	345–280
		Permian	280–225
	Mesozoic		225–65
		Triassic	225–190
		Jurassic	190–136
		Cretaceous	136–65
	Cenozoic		65–present
		Tertiary	65–1
		Quaternary	1–present

most likely would have included He and simple hydrides such as those now found on Jupiter, Saturn, Uranus and Neptune, with CH_4 (methane), NH_3 (ammonia) and water vapor being the most notable. Details of the Earth's primary atmosphere are very difficult to determine simply because there is very little evidence of the primary atmosphere left to investigate.[24]

As the solar nebula began to dissipate, so too did the Earth's primary atmosphere. Atmospheric gases escaped because the early Planet's gravity was not strong enough to hold lighter gases. Gases were also driven off by the solar wind, a stream of plasma released from the upper atmosphere of the Sun containing high-energy electrons and protons. This was a consequence of the young, premature Planet not yet having a differentiated core (a solid inner and liquid outer core) to create a planetary magnetic field capable of deflecting the solar wind.[24] Other events soon followed that profoundly changed the Planet and its atmosphere.

1.2.2 The Secondary Atmosphere of the Earth

The loss of gases from the primary atmosphere was accompanied by a loss of the Planet's primordial heat into space, the condensation of water as rain and its accumulation on the surface of the cooling Planet to form lakes, seas and oceans. The interaction of water, heat and rock set the stage for the origin of life. Once the Earth's core differentiated, heavier gases were finally retained in the atmosphere, ultimately giving rise to the secondary atmosphere.

Earth's secondary atmosphere first appeared at ~4.5 Ga, soon after the Earth and Moon completed their formational phase, and was produced by out-gassing from volcanism together with gases produced during the late heavy bombardment of the Earth by huge asteroids.[24] The gases constituting this atmosphere were probably similar to those created by modern volcanoes, likely including H_2, water, CO (carbon monoxide), CO_2, N_2, S_2 (sulfur), SO_2 (sulfur dioxide) and Cl_2 (chlorine). The secondary atmosphere was probably several times denser than the present atmosphere and almost certainly was dominated by CO_2, a major greenhouse gas. A tremendous greenhouse effect must have accompanied this atmosphere, especially since the Sun was ~30% dimmer at this time and supplied less solar radiation to warm the Planet.[25,26] Such a warming effect would have been necessary to maintain water in a liquid state and ensure that Planet would not become a frozen wasteland without any hope for the earliest forms of life to take hold.[27] With the exception of one cold glacial period phase at ~2.4 Ga, the geological record reveals a warm surface during the Archean Era (the geological era 4.5–2.5 Ga and part of the Precambrian Supereon; see Table 1.1) suitable for sustaining life. Free O_2 began to appear in the atmosphere late in the Archean, apparently produced by photosynthesizing cyanobacteria (referred to as the Great Oxygenation Event).

1.2.3 Evolution of an O_2-Rich Atmosphere

The evolution of an O_2-rich atmosphere was intimately coupled to the evolutionary history of life. As the Planet's biosphere and atmosphere co-evolved over the following billions of years, free O_2 created from photosynthesis began to dominate the chemistry of the atmosphere. Some O_2 was transformed into O_3 (ozone) in a process using UV radiation from the Sun, and a slow but progressive accumulation of O_3 began in the upper atmosphere. During this same period, the atmospheric concentration of free CO_2 progressively decreased and stabilized at its present level. The decreasing CO_2 levels appear to have been a response of the environment to the Sun's steady increase in luminosity in order gradually to attenuate greenhouse warming at the same time. The carbon cycle, which contains both biological and geological processes, began early in the evolutionary history of life as living systems took over the production of organic matter and O_2 began to regulate the balance of carbon between the atmosphere and the oceans. The cycle helped to regulate the Earth's surface temperature by balancing the CO_2 output from volcanoes and weathering and the burial of organic matter in sediments. Clearly, the evolution of life was central for creating the unique conditions for habitability on Earth; life regulates the global environment.[28] As shown in Table 1.2, comparisons of the Earth's atmosphere today with those of its nearest neighbors, Mars and Venus, illustrate this concept. Our nearest

Table 1.2 Atmospheric pressure and composition of the earth in comparison with its nearest planetary neighbors. Adapted from Mojzsis.[27]

Planet	Pressure/ bar	CO_2/% v/v	N_2/% v/v	^{36}Ar/% v/v	H_2O/% v/v	O_2/% v/v
Venus	92	96.5	3.5	0.00007	<0.00003	Trace
Earth	1.013	0.033	78	0.01	<3	21
Mars	0.006	95.3	2.7	0.016	<0.0001	Trace

neighbor planets have negligible amounts of O_2 in their atmospheres, both of which are dominated by CO_2. This would have been the fate of the Earth's atmosphere also if were not for life appearing and changing the atmosphere to keep the Planet habitable. Lastly, the constant rearrangement of continents by plate tectonics influenced the long-term evolution of the atmosphere by transferring CO_2 to and from continental carbonate stores. The theoretical decrease in atmospheric CO_2 levels over geological time, based on the model of Kasting,[29] is illustrated in Figure 1.1.

Evidence from paleosols (ancient soils) and also a variety of other geologic evidence indicates that beginning ~2.5 Ga ago, sedimentary rocks began to become increasingly affected by the rising concentrations of free atmospheric O_2 and appeared red in color as if "rusted." Resulting from the oxidation of iron in the rock, the "rusted" appearance is possible only in the presence of O_2. Atmospheric O_2 concentrations are believed to have increased rapidly at about this time as a consequence of more O_2 being produced through photosynthesis than was consumed by chemical reactions within the atmosphere, oceans and rocks. A threshold O_2 concentration was finally reached that transformed the earlier reducing atmosphere to an oxidizing atmosphere. At about the same time, more complex microbial life evolved in response to the higher O_2 concentrations, including eukaryotes, and a powerful O_3 screen began to form in the upper atmosphere when the atmospheric O_2 level reached ~1% of today's level. The theoretical increase in atmospheric O_2 levels over geological time according to the model of Kasting[29] is shown in Figure 1.2.

1.2.4 Present-Day Composition and Structure of the Atmosphere

The chemical composition of the present-day atmosphere is shown in Table 1.2. Water vapor concentrations vary significantly from ~10 parts per million by volume (ppmv) in the coldest regions of the atmosphere to as much as 50 000 ppmv (5% by volume) in hot, humid air masses (the value in the table is an average value). Many substances of natural origin may be present as aerosols, including dusts of different mineral and organic compositions, pollens and spores, sea spray and volcanic ash. Various industrial pollutants may also be present as gases or aerosols, including chlorine (in both elemental Cl_2 and molecular forms), fluorine compounds and elemental mercury

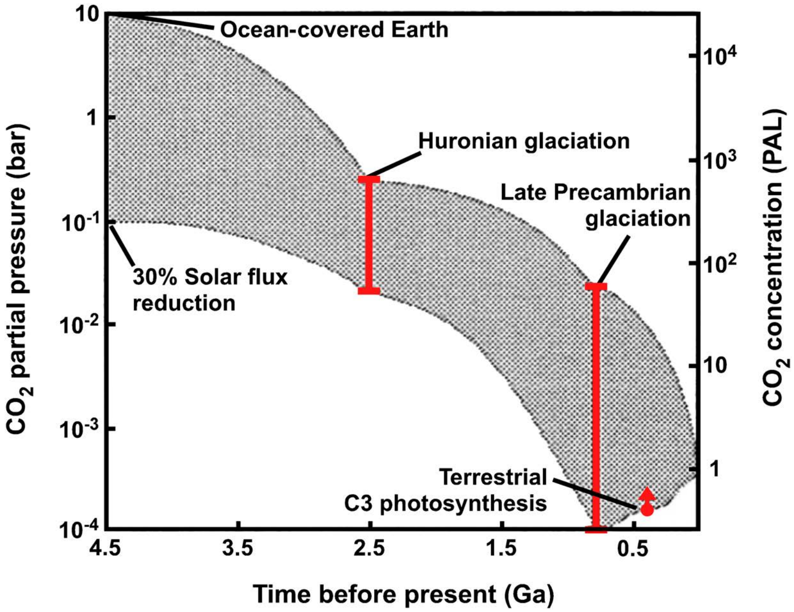

Figure 1.1 Estimated CO_2 concentrations in Earth's atmosphere over geological time in response to the steady increase in solar luminosity. The shaded areas represent the range in CO_2 concentrations required to keep the Earth's surface warm enough for liquid water to exist in the presence of the lower solar output. The figure starts ~4.5 Ga with an ocean-covered Earth and a solar flux ~30% lower than that today and extends to present-day conditions. Major glaciation periods are indicated, as is the rise in terrestrial plants and C_3 photosynthesis (the most common type of photosynthesis where CO_2 is first incorporated into 3-phosphoglycerate, a three-carbon or C_3 compound). PAL is the present atmospheric level. Adapted from Kasting.[29]

vapor. Sulfur compounds such as H_2S (hydrogen sulfide) and SO_2 may be derived from natural sources or industrial air pollution.

In general, both air pressure and density decrease with increasing altitude in the atmosphere. Temperature, however, has a more complex relationship with altitude and may remain constant or even increase with altitude in some regions. However, because the relationship of temperature with altitude is generally constant and recognizable through measurements such as balloon soundings, temperature behavior provides a useful means to distinguish between atmospheric layers. Based exclusively on temperature, the atmosphere can be divided into five principal layers or atmospheric stratifications: the troposphere, stratosphere, mesosphere, thermosphere and exosphere. The order of these stratifications is illustrated schematically in Figure 1.3 along with the atmospheric temperature profile. Of these, only the troposphere, stratosphere and mesosphere are considered part of the biosphere[30] and are relevant to aerobiology.

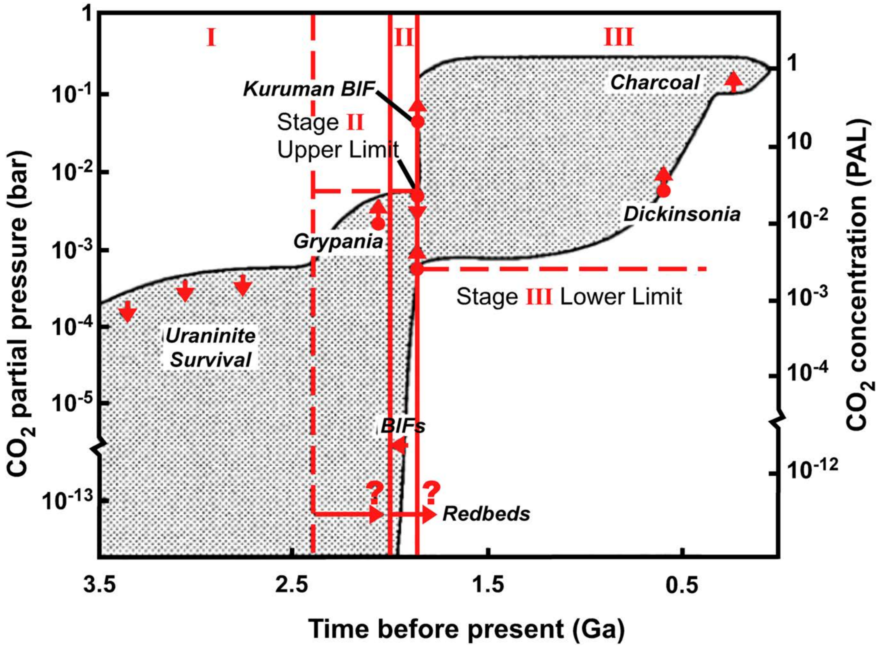

Figure 1.2 Estimated free O_2 concentrations in Earth's atmosphere over geological time. The shaded areas represent the range of possible O_2 concentrations from model calculations and investigations of paleosols (ancient soils), fossil organisms and marine sediments that only form in the absence of O_2. The sediments are preserved as banded iron formations (BIFs) and only appear in the geological record up to ~1.8 Ga. The point labeled Kruman BIF represents a lower limit for the partial pressure of O_2 (pO_2) based on a paleoweathering rate analysis (Hollard and Beukes, 1990). Solid vertical lines represent the most probable dates for transitions between three unique stages in the development of the atmosphere and ocean as O_2 reservoirs:[137] (I) the atmosphere and entire ocean were anoxic, with localized O_2 oases in highly productive regions of the surface ocean, (II) the atmosphere and surface ocean were O_2-rich and the deep ocean remained anoxic and (III) both the atmosphere and ocean were O_2-rich. The dashed vertical line indicates an earlier date for the beginning of stage II consistent with redbed (sedimentary rocks appearing red from the presence of ferric oxides) data[138] and the appearance of *Grypania* (a corkscrew-shaped organism from the Proterozoic era likely to have been a photosynthetic alga). The dashed horizontal lines represent the theoretical pO_2 limits derived from the three-stage model. Additional constraints can be imposed on the upper pO_2 limit during stage I when considering the survival of uraninite and other detrital grains[139] that rapidly weather in the present-day atmosphere. The lower pO_2 limits, labeled Dickinsonia and Charcoal, are from Runnegar[140] and Jones and Chaloner,[141] respectively. PAL is the present atmospheric level. Adapted from Kasting.[29]

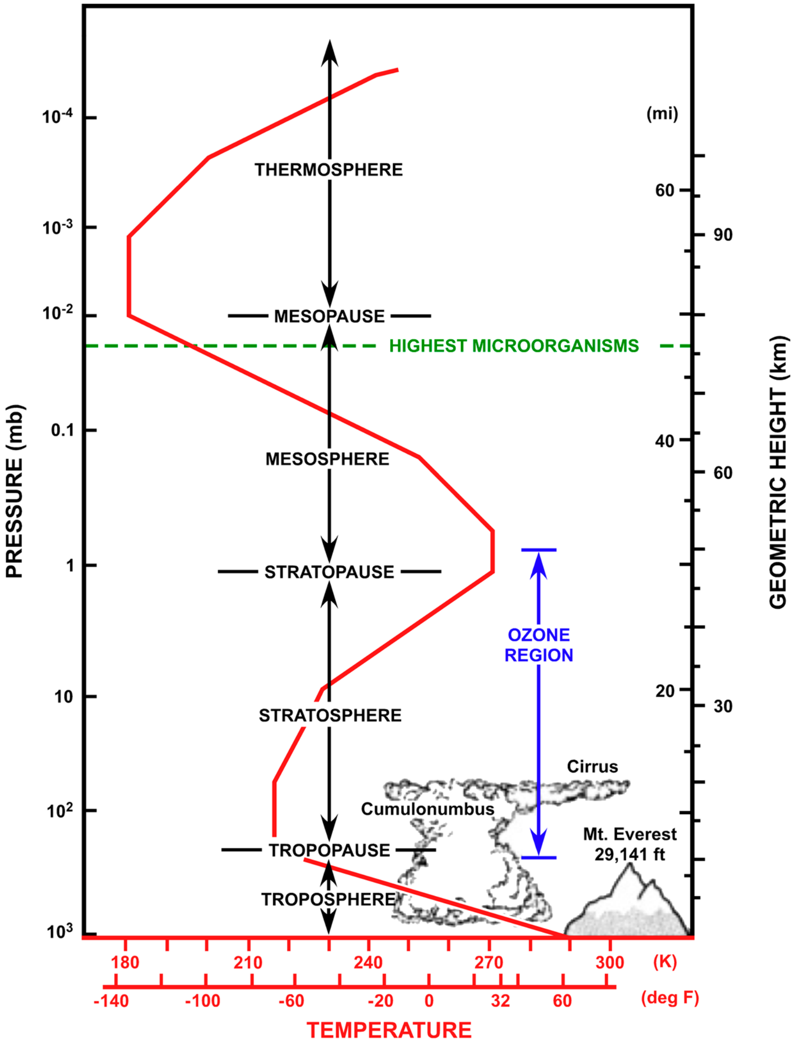

Figure 1.3 Schematic structure and temperature profile of the Earth's atmosphere. The geometric height above sea level is shown in kilometers (km) and miles (mi). Temperature is shown in kelvin (K) and degrees Fahrenheit (deg F), while pressure is shown in millibars (mb). Illustrations of cumulonimbus and cirrus clouds, and also Mount Everest, are included as vertical scale references. The horizontal dashed line at 77 km represents the highest altitude at which living microorganisms have been found.[30]

The troposphere extends from the Earth's surface to an average height of ~12 km (~40 000 ft) ASL (above sea level), although it actually varies from ~8 km (~26 000 ft) ASL at the Poles to ~17 km (~56 000 ft) ASL at the Equator, with some local variations due to weather. This atmospheric stratification contains the Planet's boundary layer (0–2 km or ~0–6600 ft ASL), where air