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Changes in terrestrial natural radiation levels over the history of life

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Background radiation dose has changed throughout Earth's history. Through geologic time, the uppermost layers of Earth became steadily enriched in radioactive ^{40}K, U, and Th. As this enrichment occurred, radioactive decay reduced the radioactivity concentrations in the crust. The result is that radiation levels from geologic and internal biologic emitters (^{40}K) likely peaked about 2 billion years ago (Ga) at a dose rate of about 7 mGy yr^{-1}, while radioactive decay of ^{40}K reduced radiation dose from internal emitters by a factor of 10 since life first appeared [1]. Throughout Earth's history radiation dose from galactic cosmic rays (GCRs) has likely increased by a factor of nearly 10 while dose from solar charged particles has dropped by a factor of about 8 through the last 4 Ga as a result of solar evolution. Solar UV emissions have increased steadily, but the formation of Earth's ozone layer about 2 Ga resulted in the flux of ionizing UV dropping by a factor of over 400 through time. In addition to these steady changes, episodic events such as very large solar flares, nearby supernovae, and even gamma ray bursts have the ability to produce short-lived sea level radiation doses on the order of 1 Gy, and such events are expected to occur once or twice per species lifetime [2,3]. It is possible that these events exert a selection pressure in favor of resistance to radiation damage among organisms living at or near Earth's surface.

Changes in background radiation levels, atmospheric oxygen concentrations, and other environmental mutagens through geologic time may have influenced the manner in which modern organisms respond to DNA damage. In particular, changes in oxygen concentrations also affect rates of radiogenic DNA damage because of oxygen's role in enhancing radiation damage [4]. Such changes may have influenced evolution for a wide variety of organisms. The specific environment in which ancient organisms lived (e.g., aerobic vs. anaerobic or photic zone vs. deep marine) likely affected their DNA damage rate and, hence, their individual exposures to DNA-damaging agents at times in the past [5].

RADIOACTIVITY IN THE ENVIRONMENT
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1. Introduction

Radiation is one of the many DNA-damaging agents to which life has been exposed since it first appeared on Earth. The sources of natural background radiation include U, Th, and ^{40}K in the rocks and soil; the radioactive fraction of potassium that is part of our essential biochemistry, and radiation from cosmic sources. The damage done to the genome is related not only to the actual types and amounts of radiation to which life is exposed, but to other modifying factors, as well. The foremost of these is free oxygen, which strongly enhances radiogenic DNA damage. Earth's ozone layer is made of oxygen and provides protection against ionizing wavelengths of UV radiation that would otherwise damage organisms at Earth's surface. Therefore, the chemical evolution of the atmosphere (most significantly, the addition of oxygen) is at least as important a factor in the history of radiation damage as is any other factor. This research touches on all of these sources of radiation damage.

1.1. *Radiation dose from biological emitters*

Early life is thought to have arisen in the ancient oceans, probably on contact with the seafloor. Although early organisms probably became free-floating early in the history of life, it is likely that the seafloor remained a favored habitat and, indeed, many organisms continue to live in and on the ocean's floor. In addition, fossil evidence strongly suggests that the earliest life quickly became colonial, forming relatively thick algal and bacterial mats and stromatolites. Even though the earliest organisms may have been sheltered from other sources of radiation (i.e., UV and cosmic radiation), they could not have escaped radiation from their internal biochemistry or the seafloor on which they lived. Life, both at its inception and throughout most of its history, has been exposed to significantly higher radiation levels than exist today from these inescapable sources of radiation exposure.

The only variables in dose from biological ^{40}K are the time at which the dose rate is calculated and the organism's K concentrations. If we assume a K concentration of 250 mmol L^{-1},[1] we find that the radiation dose rates from internal ^{40}K have decreased steadily since life evolved from about 5.5 to about 0.70 mGy yr^{-1} at present, as shown in Fig. 1.

1.2. *Radiation dose from geologic emitters*

Though geologic time, Earth's U, Th, and K were concentrated into Earth's crust because large ions such as these are preferentially partitioned into the magma that erupts at Earth's surface. As a result of this process, the concentrations of U, Th, and K in Earth's crust have increased. At the same time, however, all three elements have undergone radioactive decay. The result of these competing processes is that radiation dose from geologic emitters remained nearly steady at 1.6 mGy yr^{-1} until about 2 Ga and has dropped steadily since that time [1]. This reflects the partition of radionuclides into the continental crust (via continental crust formation) at a rate similar to the decay rate during this period.

The calculated radiation dose from all geologic materials was about twice that of current levels when the first continental crust formed about 4 billion years ago (Fig. 1). This dose

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[1] A concentration of 250 mmol L^{-1} is used as an example of an average bacterium. See [1] for a more complete discussion of K-concentrations and resultant doses through geologic time.

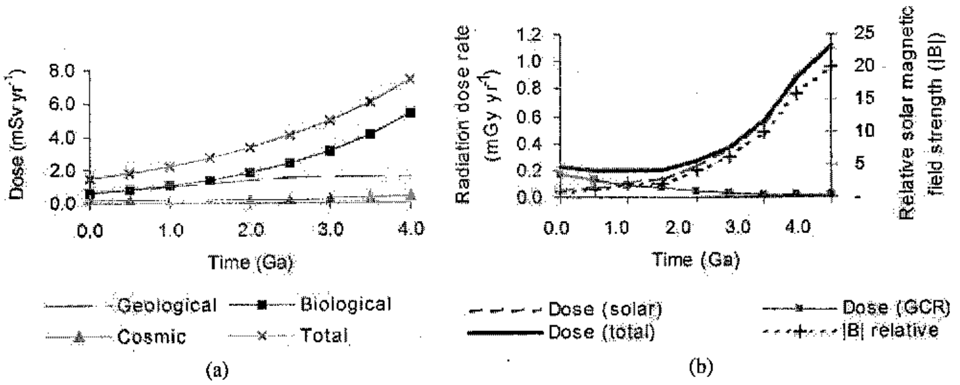

Fig. 1. (a) Changes in background radiation levels through time. The x-axis starts at the present day and goes to 4 Ga. (b) Shows changes in cosmic radiation dose on an expanded scale.

was virtually identical to that from mafic[2] rocks at that time because very little felsic crust existed. As the continental crust formation rate slowed, radiation levels began to fall, reflecting the decay of U, Th, and, most importantly, ^{40}K. The modeled radiation level at present (0.66 mGy yr^{-1}) is higher than the 0.28 mGy yr^{-1} typically attributed to dose from geologic materials (NCRP, 1987) because soils (included in the 0.28 mGy yr^{-1} figure) are usually deficient in U, Th, and ^{40}K compared to rocks, and the calculated doses reflect the chemical composition of rocks alone. It is likely that soils resembling those at present did not begin to form until the colonization of land by large plants about 380 million years ago. Before this time soils would be expected to closely resemble, both chemically and radiologically, the underlying rock. The calculated dose does compare favorably with doses derived from radionuclide composition information reported in Eisenbud and Gesell [6] and UNSCEAR [7] (0.71 and 0.77 mGy yr^{-1}, respectively).

1.3. *Radiation dose from solar charged particles and galactic cosmic rays*

Changes in cosmic radiation exposure clearly fall into two major categories: long-term, gradual changes that stem from continuing physical and chemical processes and short-term events that occur infrequently and aperiodically. The most important factors controlling extraterrestrial radiation dose experienced on Earth include:

- Solar evolution and its effects on UV emission, solar charged particle flux, and galactic cosmic ray flux.
- Long-term changes in the chemical composition of Earth's atmosphere and the effects on UV flux and on radiogenic DNA damage.
- Long-term changes in the terrestrial magnetic field, including the impact of occasional magnetic field reversals on the formation of cosmogenic radionuclides.
- Short-term effects of large solar flares on sea level radiation exposure.

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[2] Mafic rocks have high concentrations of magnesium and iron, and low concentrations of U, Th, and K. Basalt is an example of a mafic rock. Felsic rocks are rich in feldspars, quartz, muscovite, and feldspathoids and high concentrations of U, Th, and K. Granite is an example of a felsic rock.

- Short-term effects of prompt gamma rays from supernovae and gamma ray bursts and the radiation dose generated at sea level from these events.
- Intermediate-term (i.e., over several months) radiation exposure from the decay of supernova-produced radioactivities.

The Sun contributes to terrestrial radiation dose by emission of charged particles (the solar wind) and by the action of its magnetic field, which helps to exclude high-energy galactic cosmic rays (GCR) from the inner Solar System. Galactic cosmic rays are more effective than solar charged particles at producing sea level radiation dose because of their higher energies, so the effect of changes in solar activity (which affects solar magnetic field strength) on sea level radiation dose is not simple. This is shown in Fig. 1b.

Over the Sun's history, solar activity has dropped steadily [8] as its rotation has slowed. This, in turn, means that the solar wind has weakened and solar charged particles have had lesser importance in sea level radiation dose while GCRs have become steadily more important [9,10].

Calculations show that the relative contributions of solar and galactic cosmic rays to sea level radiation exposure have changed continuously through time and that, on the early Earth, solar cosmic rays were a more important source of radiation than were GCRs [9,10]. The lowest calculated cosmic radiation dose from these combined sources occurred about 1 billion years ago at a value of about 0.2 mGy yr^{-1} (from a peak value of almost 1.2 mGy yr^{-1} in the earliest Solar System) before gradually increasing to modern values. However, we note that, even at the highest levels, cosmic radiation played only a minor role in the overall background radiation "picture" at any time in the past. Changes in radiation dose from cosmic, geologic, and biological sources are summarized in Fig. 1a and 1b.

1.4. *Ultraviolet radiation dose*

The surface of the Sun behaves, to a reasonably good first-order approximation like a black body in that its spectrum depends primarily upon its temperature. The presence of absorption lines for some elements and emission lines for others causes the Sun to depart from the ideal, but these effects are not considered in this paper. Over its lifetime, the Sun has become gradually hotter with a corresponding spectral shift to shorter wavelengths, so UV emissions today are much higher than in the past.

At the time when life appeared at 4.0 Ga the luminosity of the Sun was approximately 70% of its present luminosity [11,12]. Plank's law states that the energy emitted in any wavelength is related to the black body curve. According to Planck's Law, the energy emitted in a specific wavelength (for example, the UV emission) of a black body is proportional to $1/(e^{1/T} - 1)$. As the Sun has become hotter, its UV emissions have increased as well. In fact, UV emissions in the early Sun, when the Sun's surface temperature was 90% the value today, were about 50% current levels. Current solar evolution models suggest that the Sun's surface temperature has risen nearly linearly with time [8]. Therefore, UVB and UVC emissions have changed as well, increasing to modern levels as the Sun has evolved.

Increases in emissions of ionizing UVB and UVC, however, only address the source term. Of equal importance is to determine the amount of radiation reaching Earth's surface. The primary UV shield is ozone. Before the formation of Earth's ozone layer, UVB and UVC reached Earth's surface almost unattenuated. Thus, surface UV flux was significantly higher in the distant past than it is today even with lower source emissions.

A series of rocket-borne experiments have provided information on the solar UV spectrum in space and the absorption cross-section for ozone across this spectrum. Others have reported on the average column density of ozone molecules in the atmosphere [13]. These data can be combined to arrive at the fraction of incident UV radiation that reaches sea level, assuming that scattering and absorption by other atmospheric constituents is negligible. The resulting sea level photon flux for each wavelength is then in units of photons $\mathrm{cm}^{-2}\,\mathrm{s}^{-1}$.

The photon flux is converted to an energy flux by calculating the energy of individual photons. Multiplying the photon energy by the photon flux yields an energy flux at sea level. Because the UV spectrum is reported in wavelength bands, the central wavelength of each 5 nm band was used for these calculations. Summing the UV flux shows that, today, the solar UV flux is about 14 000 ergs $\mathrm{cm}^{-2}\,\mathrm{s}^{-1}$ in space and is attenuated to about 29 ergs $\mathrm{cm}^{-2}\,\mathrm{s}^{-1}$ at sea level [9].

In the past, Earth had noticeably less oxygen in the atmosphere and correspondingly less ozone. This allowed high levels of UV to penetrate to sea level. To calculate sea level UV flux in the past, ozone concentrations were assumed to be directly proportional to atmospheric oxygen levels at that time (Cockell, personal communication). For example, today's atmosphere contains about 21% oxygen and has a column density of about 8×10^{18} molecules of ozone cm^{-2}. However, a billion years ago, the atmosphere had only about 15% today's oxygen concentrations (or about 3% oxygen) [12], giving it an ozone column density of about 1.2×10^{18} molecules cm^{-2}. Summing the photon and energy flux at sea level a billion years ago, we find that it was about 2200 ergs $\mathrm{cm}^{-2}\,\mathrm{s}^{-1}$ and the incident photons were primarily of wavelengths between 280 and 300 nm [9].

Another factor that must be taken into account is the changing solar spectrum over time. As noted above, the Sun has become steadily hotter as it has evolved, emitting correspondingly higher levels of UV radiation. We assume that the early (4 Ga) Sun was 70% as luminous as today's Sun and that solar luminosity and temperature increased in a linear fashion in the intervening time [8]. The changes in solar luminosity were used to derive the Sun's surface temperature that was, in turn, used to determine the flux of UV photons in each wavelength band at that time in the past. These calculations show that the early earth was subjected to significantly higher levels of ionizing UV radiation prior to the formation of the ozone layer. This conclusion is hardly a surprise and has, in fact, been reached by many in the past [14,15]. These calculations also show that UV flux on the earliest earth was approximately 430 times as intense as on Earth today. This value compares favorably with Cockell's ratio of 470 times the relative DNA damage rates to early life from UV radiation [14]. Cockell also noted that other factors, including other atmospheric gases, particulates, or sulfur compounds may have helped screen early life from UV irradiation, but their presence cannot be known with any degree of certainty. Changes in sea level UV flux are shown in Fig. 2.

The DNA-weighted UV irradiance at sea level today is about 1 erg $\mathrm{cm}^{-2}\,\mathrm{s}^{-1}$. Therefore, earliest life (if exposed at Earth's surface) would have received an irradiation of over 400 ergs $\mathrm{cm}^{-2}\,\mathrm{s}^{-1}$. This is equivalent to an *E. coli* mutation doubling dose every quarter second [16], which is much too high for a living organism to survive. Since life exists today, it is evident that early life found a suitably shielded habitat, either in the deep sea, beneath a surface layer of sediments, or some other UV-opaque material. However, it is likely that many

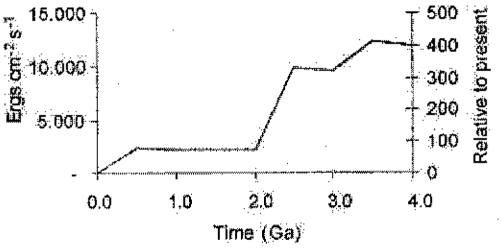

Fig. 2. Changes in sea level flux of UVB and UVC through time. The sharp drops are due to oxygenation of the atmosphere and the slight rises between these drops in flux are due to the effects of solar evolution.

dominant life forms on the early Earth were photosynthetic, especially after about 3 billion years ago. Accordingly, it is highly probable that these organisms were still exposed to levels of UV radiation significantly higher than those experienced by modern organisms [17]. In fact, if we can draw corollaries from similar organisms that are extant today, it is likely that many early photosynthetic organisms lived in waters less than a few meters in depth, placing them well within the zone into which UVB and UVC can penetrate [12,14,18]. Other organisms, such as stromatolites may have evolved the ability to survive in the photic zone by developing UV-resistant outer (and upper) layers that protected the more sensitive cells beneath [12,19]. Survival strategies used by such organisms have been previously discussed in the scientific literature (see, for example, [15]) and are not discussed further here. Cockell also pointed out that the DNA-weighted UV flux in the ancient oceans, prior to the formation of an ozone layer, would have decreased to roughly present-day surface levels at a depth of about 30 m, while he and others suggest the early oceans may have been covered in part by UV-opaque molecules that would have served to help protect the life beneath [20,21].

2. Radiation dose from episodic cosmic events

Some have speculated that occasional events such as supernovae, gamma ray bursts, or solar "super-flares" may have contributed sufficient radiation dose to organisms at Earth's surface to have caused mass extinctions [22–25]. Calculations suggest otherwise because of the rarity of catastrophic cosmic events near enough to earth to deliver lethal radiation dose to our planet's surface, but it is still possible for cosmic events to affect terrestrial life [26,27].

Radiation exposure at Earth's surface from gamma ray bursts is likely to reach levels of about 1 Gy approximately once per species lifetime [26], but supernova emit too little prompt gamma radiation to have a significant effect on sea level radiation levels. On the other hand, supernovae produce approximately 10^{28} kg of radioactive ^{56}Ni when they explode. The decay of this radioactive nickel to stability (via ^{56}Co) releases nearly 10^{43} J of gamma energy over the course of a few years. Although over 90% of this energy is absorbed by the supernova remnant, the remainder escapes into space and can produce a radiation dose of up to 1 Gy at Earth's surface with a mean interval of about 5 million years [27].

Two lines of evidence point to periodic solar "superflares" occurring on similar time scales [4,28]. Superflares emit substantially more energy than normal solar flares and are also capable of producing very high (about 1 Gy) radiation levels at sea level approximately once per species lifetime. Accordingly, we feel is safe to say that the vast majority of organisms will never experience such high radiation levels, but each species will. Because of this, it is possible that even such infrequent events can contribute towards species maintaining the ability to repair radiation damage in spite of steadily declining terrestrial levels through time.

We also note that radiation dose in space from these events is likely to be sufficiently high as to place some constraints on the ability of living organisms to travel between planets or between planetary systems. In order to survive a journey of several tens of millions of years, organisms would need to reside in bodies of rock or ice at least several tens of cm in diameter [26,27]. Bodies of this size are relatively rare, suggesting that interplanetary "seeding" may be similarly rare.[3]

It is worth noting that there is a high probability that nearby supernovae have frequently produced sufficient UV flux to have had a major impact on terrestrial life. Due to intense UV emissions from supernovae, it is probable that Earth experiences a sea level UV dose sufficient to cause a doubling of the background mutation rate with a mean interval of about 200 000 years (Scalo, personal communication). The mean interval between events that would contribute a UV flux that is greater than that of the Sun is only a few thousand years.

3. Modifying effects of changes in the terrestrial atmosphere

The terrestrial atmosphere has changed in composition and quantity since Earth first formed. Of all the atmosphere's constituents, the most important from the standpoint of this research is the presence of free oxygen in the atmosphere because of oxygen's role in forming the ozone layer and its role as a powerful modifier of radiogenic DNA damage. The following discussion summarizes more detailed information found in [3].

The earliest atmosphere was likely anoxic, and oxygen levels increased in steps at distinct times in the past. The first step occurred about 3 billion years ago, when oxygenic photosynthesis was "invented" by early cyanobacteria [29]. Although the great majority of this oxygen reacted with reduced ions in Earth's oceans, atmosphere, and crust, it is likely that trace amounts remained in the atmosphere and that larger amounts were dissolved in seawater in "oxygen oases"; isolated or restricted basins that were not in equilibrium with the bulk ocean. Accordingly, although background radiation levels were nearly ten times those found today, radiogenic DNA damage rates were only about 2 to 2.5 times present levels.

About 2 billion years ago, when the reduced ions had been oxidized, oxygen began to accumulate in the atmosphere and oceans, leading to a sharp increase in radiogenic DNA damage. This damage decreased with decaying radiation levels until the next sharp increase in atmospheric oxygen levels about 440 million years ago, when plants began colonization of land. From that time until the present, radiogenic DNA damage rates have dropped steadily along with background radiation levels, as shown in Fig. 3.

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[3] Consider, for example, that the putative martian meteorite ALH84001 was in space for about 16 million years to travel the 75 million km from Mars' orbit to that of the Earth.

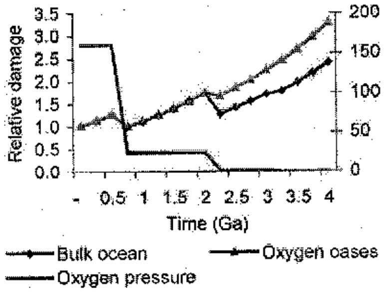

Fig. 3. Changes in atmospheric oxygen concentrations and radiogenic DNA damage rates through time.

The effects of increasing atmospheric oxygen levels on sea level UV flux, discussed earlier, was even more profound.

4. Other environmental mutagens

There are, of course, many environmental mutagens, all of which have changed through time. These include the evolution of eukaryotic life, which exposed cells to the leakage of free radicals from mitochondria, changes in dissolved oxygen levels, which led to oxidative DNA damage even in the absence of radiation, and the likely presence of other, as yet unknown, DNA damaging agents in the ancient oceans. To fully understand the response of modern organisms to DNA insult, we must better understand how all of these factors have changed with time. We have made preliminary efforts to do so [5], and are now undertaking more detailed calculations. We also realize that not all organisms will be exposed to all mutagens, so it may also be necessary to determine the "lifestyle" of a particular organism and its evolutionary antecedents in order to better appreciate the manner in which it will respond to DNA damage. This is obviously far beyond the scope of this paper, and will make for many years of fascinating research. The results of our initial work are presented in Fig. 4 and in previous work [6].

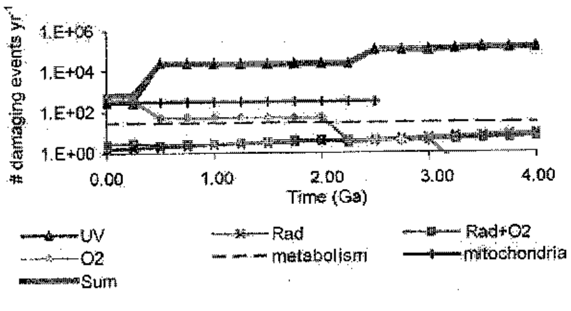

Fig. 4. Changes in environmental mutagens and mutation rates through time [5].

5. Discussion and conclusions

Many of the DNA damage repair mechanisms in modern organisms are conservative [30]; they are very similar in widely disparate kingdoms such as eubacteria, archaebacteria, and animalia (the animal kingdom).

This observation supports the idea that such repair mechanisms evolved only once in the common ancestor to all modern life forms, before life diverged to form the modern kingdoms. If this is the case, then the mutation repair mechanisms in humans likely has its evolutionary roots in an environment that was far more mutagenic than today's, and may have retained the ability to successfully repair levels and rates of DNA damage in excess of those found today. This possibility gives a geological and historical context to the idea of a threshold level, below which life's cellular repair mechanisms can adequately repair radiation damage with little or no expected harmful effects to the organism. The discovery that adaptive response to radiation can be induced by exposure to elevated levels of background radiation, such as those found in Ramsar, Iran [31], lends some credence to this speculation.

The earliest life consisted of prokaryotes, small cells with few organelles and no nucleus. Some prokaryotes (archaebacteria) can live in extreme environments not inhabited by other kingdoms of life, although organisms from these domains of life are common in virtually all environments on Earth. Eukaryotes are thought to have evolved about 2 billion years ago [32] as the result of symbiosis between prokaryotes [33]. Eukaryotes are larger and more complex than prokaryotes, containing numerous organelles and a nucleus containing genetic information. Fungi, protists, plants, and animals are composed of eukaryotic cells.

Eukaryotic cells are generally more sensitive to the effects of radiation than are prokaryotes. This sensitivity could reflect the greater complexity of eukaryotic cells, making their functioning easier to disrupt; the relatively greater chromosome volume, giving more "targets" for mutating events; their evolution in a background radiation field lower than that in which prokaryotes evolved; some combination of these; or another cause entirely. In any event, it is interesting to note that many mutation repair mechanisms are shared by both prokaryotic and eukaryotic cells, while others are unique to each kingdom of life [34].

The United Nations Science Committee on the Effects of Atomic Radiation published a table showing lethal radiation dosage ranges for a number of phyla [35]. In general, more recently evolved organisms show higher sensitivity to the effects of radiation as evidenced by lower lethal dose ranges. It is tempting to claim that this demonstrates the evolution of these organisms in successively lower radiation fields over time. However, with the possible exception of eukaryotes noted above, this is likely an oversimplification because multi-cellular life forms evolved quickly with respect to the half-life of ^{40}K (the primary source of radiation exposure), so dose rates did not change significantly between the evolution of molluscs (about 550 million years ago) and the first mammals (about 200 million years ago). Halliwell and Aruoma [36] similarly note that in vivo $^{\bullet}$OH formation resulting from exposure to background radiation and reaction of H_2O_2 with metal ions may have helped stimulate the development of some DNA repair systems. If this is the case, it may be possible for these repair mechanisms to have retained the ability to efficiently and accurately repair higher rates of DNA damage than exist at present.

In addition, there may be a qualitative difference between DNA damage from even low-LET radiations and from other mutagens [37,38]. This suggests that it is possible that the response of modern organisms to radiation insult may, in part, reflect the mutagenic environment in which these repair mechanisms evolved.

However, in order to fully assess what capabilities current repair mechanisms possess, it is necessary to develop a more complete understanding of the environment in which they have evolved since first appearing in our most ancient ancestors. For that reason, it is possible that the changes in natural radiation levels through the history of life on Earth may help in better understanding the ability of modern organisms to repair mutations due to exposure to background or anthropogenic radiation.

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