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L'ÉNERGIE ATOMIQUE DU CANADA LIMITÉE

RADIATION AND THE EVOLUTION OF LIFE

Radiations et l'évolution de la vie

N.E. GENTNER and D.K. MYERS

Prepared for talks given by N.E. Gentner at science teachers' seminars in Winnipeg, 1979 October 19, and in Chalk River, 1980 March 29.

Chalk River Nuclear Laboratories Laboratoires nucléaires de Chalk River

Chalk River, Ontario

August 1980 août

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Health Sciences Division
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Résumé

On passe en revue: (a) la nature de différentes formes de radiation; (b) l'énergie rayonnante venant du soleil qui atteint la terre; (c) le rôle de cette énergie dans l'évolution chimique prébiotique; (d) les idées actuelles sur les origines de la vie; (e) la dépendance des organismes vivants de l'énergie rayonnante; (f) les mécanismes responsables de l'évolution de la vie tant du point de vue de la génétique moderne que de la biologie moléculaire; (g) les conséquences biologiques des modifications engendrées dans les substances génétiques; et (h) le rôle des rayonnements ionisants dans la production des changements génétiques et dans l'évolution. En dernière analyse, les processus biosynthétiques de la vie sont actionnés par l'énergie rayonnante provenant du soleil. Cette vision d'ensemble se concentre nécessairement sur les régions de l'infrarouge, de la lumière visible et de l'ultraviolet du spectre à la sortie du soleil, étant donné que ces radiations particulières sont responsables de la plupart de l'énergie rayonnante atteignant la surface de la terre. Les rayonnements ionisants semblent avoir joué au mieux un rôle mineur dans l'évolution biologique. De petits accroissements dans les quantités de rayonnements ionisants se trouvant sur la terre ne devraient donc pas avoir d'effet significatif sur la vie ou son évolution.

Laboratoires nucléaires de Chalk River
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ABSTRACT

A general review is presented of: (a) the nature of various forms of radiation; (b) radiant energy which reaches the earth from the sun; (c) the role of this energy in prebiotic chemical evolution; (d) current ideas on the origin of life; (e) the dependence of living organisms upon radiant energy; (f) the mechanisms responsible for the evolution of life, from the viewpoint of modern genetics and molecular biology; (g) the biological consequences of alterations in the genetic material; and (h) the role of ionizing radiation in production of genetic changes and in evolution. In the final analysis, the biosynthetic processes of life are driven by radiant energy from the sun. This overview is necessarily focussed on the infrared, visible and ultraviolet regions of the solar output spectrum since these particular radiations are responsible for most of the radiant energy that reaches the earth's surface. Ionizing radiation appears to have played at best a minor role in biological evolution. Small increments in the amounts of ionizing radiation are therefore unlikely to have a significant effect on life or its evolution.

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INTRODUCTION

Any presentation on radiant energy and life should begin with the single most important fact: we live about 150 million kilometres away from a giant fusion reactor, the sun, which provides us directly with heat and light and indirectly with the food and oxygen essential to our life. Without radiation from the sun, none of us would be here.

Large amounts of energy are continuously being transported throughout the universe in the form of various types of radiation. Electromagnetic radiation from the sun is the major source of energy received by our planet, in total approximately 10^{21} kilogram-calories (kcal*) per year. To put this in perspective, although this is only one-billionth (10^{-9} of the sun's output, it is roughly equivalent to the energy produced by twenty million power stations such as the one operating at Pickering, Ontario, or one such power reactor for each ten square miles of earth's surface.

Humans have found their own practical uses for each of the various types of radiant energy. A much more fascinating story emerges, however, if we examine what nature has done with these radiations. Radiation has always been there, long before humans ever existed or discovered how to use radiation for their own benefit. Radiation is energy, and life requires energy to sustain it. In fact, the origin, evolution and present nature of life may be shown to be a consequence of radiant energy from the sun. In their turn, life processes had a profound effect on the make-up of the solar radiation penetrating to the surface of this planet.

In this presentation, we shall first describe briefly the nature of various types of radiation, and second, discuss why radiant energy is a natural life force. These interrelationships are best outlined in the context of evolution. Given the requisite energy input and the raw materials available on the primeval earth, most scientists would now agree that life on this planet and its evolution was an inevitable natural event. If these natural physical and chemical laws hold elsewhere, as expected, the whole of biology and life may be viewed as a cosmic event.

WHAT IS RADIATION?

The primary form of radiant energy with which we will be concerned is electromagnetic radiation. This energy is transported across space in small discrete packages called photons or quanta depending on whether their particle

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* 1 kcal = 4186 J. Units of energy will be expressed as kcal in this paper.

or wave property is emphasized. In space, a complete range of electromagnetic radiations is present, although most of the solar energy is carried by infrared, visible and near ultraviolet radiation.

The relationship between the energy of a photon and its wavelength is given by the equation

$$E = \frac{hc}{\lambda}$$

where h = Planck's universal constant $(1.58 \times 10^{-37}\ \mathrm{kcal \cdot s})$,
c = velocity of light $(3 \times 10^{10}\ \mathrm{cm \cdot s^{-1}})$
λ = wavelength (cm)

The intensity of light is the rate of delivery of photons. The work that a single quantum can do is determined by its wavelength: the shorter the wavelength the greater is the energy content per quantum.

It is important to understand this relationship between wavelength and energy content. Every chemical reaction, including those used in life processes, has a characteristic value for its energy of activation; this may be regarded as the amount of energy which must be put into a chemical system in order to "excite" molecules to react. An energy barrier to reaction must be overcome. To break covalent bonds generally requires about 40-90 $\mathrm{kcal \cdot mol^{-1}}$ of energy corresponding to photons with wavelengths between 700 and 320 nm. (To obtain the energy in $\mathrm{kcal \cdot mol^{-1}}$ corresponding to a particular wavelength, multiply the energy for a single photon in the above equation by Avogadro's number, i.e. 6×10^{23} molecules per mole.) For synthetic reactions, the energies of activation are generally in the range 15-65 $\mathrm{kcal \cdot mol^{-1}}$, corresponding to wavelengths of 1900-440 nm. Reactions with simpler molecules, such as those available on the primitive earth as precursors of biological molecules, generally require much higher energy. From one point of view, we might consider ourselves fortunate today: the bulk of the sun's radiation falls in the proper range to promote biologically useful and important chemical reactions. But is it effect or cause? It may well be more appropriate to consider life and radiation the other way around - that the life which developed on this planet had to employ reactions consistent with this range of energies. We shall show that solar radiation and life are intimately related, and that shorter, more energetic wavelengths were available in the distant past to build a store of organic molecules in the absence of life.

The electromagnetic radiation spectrum is continuous. Operationally, in terms of the uses man makes of it, this spectrum has been divided into various "regions". Since the energy changes with wavelength, the properties of these broad divisions are different. In order of decreasing wavelength (or increasing energy per quantum), electromagnetic radiations include the following:

(a) radio waves (wavelength ~1 mm to ~1 km), which have relatively little effect upon living organisms (although the shorter wavelengths may cause dielectric heating) and which our society uses for purposes of communication;

(b) infrared (wavelength 700 nm to 1000 nm), which carries essential heat from the sun to the earth;

(c) visible light (400 to 700 nm), to which our visual apparatus is remarkably sensitive, and which is utilized by green plants for photosynthesis, thus providing us with oxygen in our atmosphere and ultimately all our foodstuffs;

(d) near ultraviolet (UV) light (300 to 400 nm), which produces vitamin D from precursors in the skin and also produces skin tan, sunburn and skin cancer;

(e) far UV light (100 to 300 nm) which does not now reach the earth's surface because it is absorbed by oxygen and ozone in the atmosphere;

(f) X-rays (less than 10 nm), similar to those used for medical diagnostic purposes; and

(g) gamma-rays (less than 0.1 nm), similar to those used in cancer radiotherapy.

The energy of X- and gamma-ray photons is 100 to 100,000 times greater than that of visible photons; this is sufficient to enable them to penetrate the tissues of the body. A portion of such energy is absorbed in tissues; its deposition can cause chemical changes or damage to biological material. Of such damage, that deposited in the genetic material (DNA) is considered to be of the greatest biological consequence.

In addition to the above, the field of radiation biology is also concerned with certain high-speed distinct particles with a definite mass; these include alpha particles (the nuclei of helium atoms), beta particles (electrons), and protons (nuclei of hydrogen atoms). Alpha(positively charged) and beta (negatively charged) particles, as well as gamma-rays (no electrical charge), are produced during the natural disintegration of such radioactive substances in the earth as certain isotopes of potassium, uranium or thorium. These energetic particles can also cause damage to DNA and other bodily constituents and, together with X- and gamma-rays, are classified in the general category of <u>ionizing radiation</u>.

The most energetic high-speed particles in existence are the primary cosmic rays. A steady rain of such particles, primarily the nuclei of the more abundant elements in the universe, moving at nearly the speed of light, is continually impinging on the earth from all directions. The primary cosmic radiation consists of about 87% protons, 11% alpha particles, 1% heavier nuclei, and 1% electrons. The most energetic of these subatomic particles may each have a kinetic energy equivalent to that of a well-hit tennis ball and carry approximately 10^{14} times as much energy as does the alpha particle emitted during the natural radioactive decay of uranium. If it were not for the atmosphere, roughly 10,000 of these particles would reach each square centimetre of the earth's surface every hour. The study of these particles has revealed much about the origin and nature of the universe. From a biologist's point of view, however, the important factor is that these primary particles are absorbed by the earth's atmosphere, resulting in exposure of living organisms to showers of secondary cosmic radiation of much lower energy and in the continuous production of radioactive isotopes such as carbon-14 and tritium (hydrogen-3) in the atmosphere.

We see, then, that the earth is (and always has been) bathed in a sea of radiation, both from without and within.

EVOLUTION OF THE SOLAR SYSTEM

According to the nebular hypothesis for the origin of our solar system, an interstellar cloud of gas and dust collapsed into itself some 4-6 billion years ago, forming a "spinning disc". At the centre of this disc, a body formed which was so dense and hot that it ignited as a nuclear fusion reactor and became a star - our sun.

The planets are also believed to have been formed from collisions and clumping of interstellar dust. Such a coagulated core, held in orbit around the sun, would continue to sweep up enormous quantities of dust grains from the nebular disc and gradually accrete to a solid planet, possibly within only a few million years. (The current rate of influx of extra-terrestial dust to the earth is estimated to be about one tonne or 10^3 kg each hour.)

This newly formed planet then began to heat up because of gravitational collapse, meteorite impacts, and the radioactive decay of uranium, thorium and potassium. As its interior became molten, a process of differentiation into a core, mantle and crust followed; heavy materials, mainly iron and nickel, sank inwards while lighter materials rose to the outer layers (the mantle and crust). The mantle consisted largely of silicates and oxides of most of the chemical elements, including the radioactive elements uranium and thorium. All but the lightest elements (hydrogen and helium) were held by earth's gravity, and the accretion atmosphere gradually evolved into a primordial atmosphere rich in methane, ammonia and water. As the differentiated crust cooled, atmospheric water and gases condensed and oceans appeared. Chemical reactions between compounds of this primitive reducing atmosphere (to be discussed later) probably gave rise to a primordial oceanic soup of organic compounds.

A minimum date for when these events occurred has been determined by radioactive dating of rocks. The oldest rocks found to date on the surface of the earth solidified about 3.6 billion years ago, but our planet is thought to be somewhat older. Meteorites, which are essentially primitive chunks of rocks from our solar system, date back to about 4.6 billion years, as do the oldest rocks recovered from the surface of the moon.

THE SUN

The sun itself appears to be mainly a ball of hot hydrogen weighing about 2×10^{27} tonnes or three hundred thousand times the mass of the earth. The enormous output of the sun suggested to early scientists that a source of energy far more potent than chemical combustion must be operative. The sun's internal temperature is about ten million degrees Celsius. In this core, we now recognize that nuclear transmutation reactions occur; one of the main cycles converts hydrogen to helium. The energy released by such reactions is approximately one million times greater than would be obtained by combustion or burning of this hydrogen with oxygen to form water. The energy release by these nuclear fusion reactions is so efficient that the sun has an expected lifetime of 10 billion years. This "fire" is now probably about halfway through its lifetime.

There is violent activity on the surface of the sun, as evidenced by the appearance of sunspots, eruptions or solar flares, and the solar corona. Auroral displays, and "storms" in the earth's magnetic field (which disrupt radio communications), are associated with solar flares. A "solar wind", a stream of charged particles, is continuously expanding outward from the sun into space. These solar particles, like the primary cosmic particles, are mainly hydrogen and helium nuclei, but in general the solar wind is much less energetic than the cosmic particles. Most of the solar wind particles never reach the earth's atmosphere because they are deflected by the earth's magnetic field; the ionizing radiation reaching the earth's surface is due almost exclusively to cosmic rather than solar particles. However, some of these solar particles are trapped by the earth's magnetic field and form toroid-shaped radiation belts (the van Allen belts) around the earth. One belt is of high energy protons about 3,000 km above the earth, at the magnetic equator; the second is composed of energetic electrons, about 15,000 km out. The radiation contours of these belts follow the lines of force of the earth's magnetic field. Astronauts must traverse the radiation fields associated with the belts, and an important aspect of the planning for space trips involves minimizing their exposure to ionizing radiation.

Although the nature of the solar radiation output is much the same now as it was in the time before life on earth began, the particular wavelengths which actually reach the earth's surface now are different from five billion years ago. The factors affecting the nature of the radiation reaching the surface are consequences of life itself. An examination of the present radiation spectrum at various distances from the surface will let us appreciate the changes which have occurred (Fig.1). At about 50 km or more above the earth's surface, a wide range of wavelengths is present; this range essentially represents the actual solar output. The boundaries for the central 90% of this energy are 230 nm and 1,600 nm. In the upper atmosphere at present, at 22-25 km, an ozone layer strongly absorbs wavelengths of solar radiation below about 320 nm; below 290 nm this ozone layer is virtually opaque. The very energetic short wavelength UV output from the sun is thus removed. This ozone "screen" is itself formed by the interaction of solar radiation with oxygen in the upper atmosphere. The free oxygen in our present atmosphere, however, was not there originally and is almost entirely itself a product of life processes. The removal by ozone of far UV radiation, we shall see, was a crucial factor in the emergence of terrestial, as opposed to aquatic, life. Therefore, on the earth's surface at the present time, these 90% boundaries of the solar output are 320 nm and 1,000 nm (Fig.1). Below the surface of the ocean, the spectrum is further narrowed, especially in the infra-red, by absorption in sea water.

CHEMICAL EVOLUTION - THE ORIGIN OF ORGANIC COMPOUNDS

The main components of the primordial atmosphere are thought to have been methane, ammonia, water and small quantities of hydrogen. This has been described as a "reducing" atmosphere. There was little or no free oxygen since the free oxygen in our present atmosphere is predominantly a product of life.

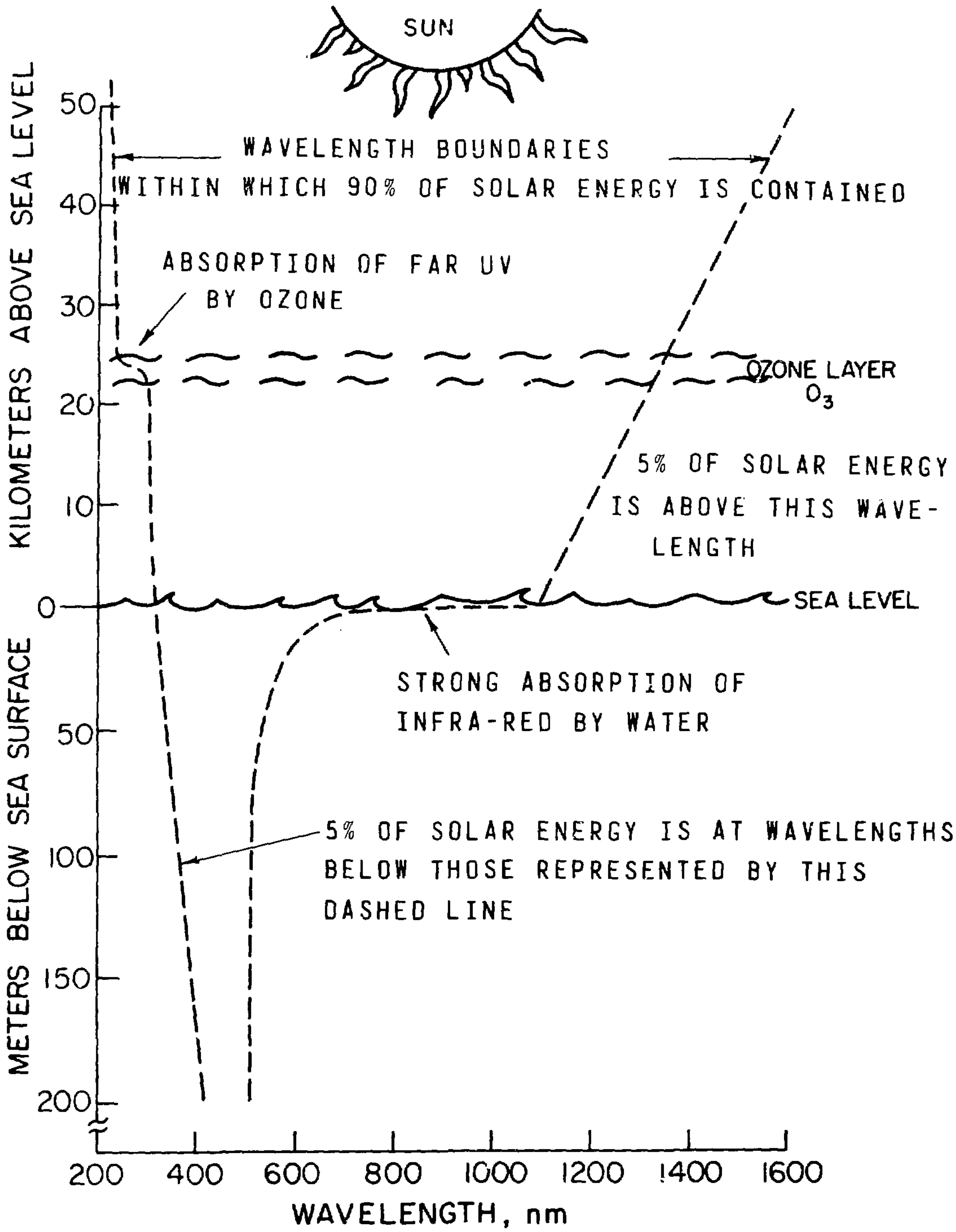


Fig.1. Solar radiation at various distances above and below the sea's surface. The left and right dashed lines represent the wavelength boundaries within which 90% of the solar output, at each level, is contained.

How did the complex compounds used in life processes, and later life itself, originate? A plausible story of chemical mechanisms has been developed for the first part of this question, and reactions by which these prebiotic syntheses might have occurred have been recently demonstrated in laboratory experiments. Considerable time was available: a wide gulf of one billion years of chemical evolution occurs between the time of formation of a sterile earth and the emergence of the first autonomous, self-replicating, living organism.

These organic compounds which we associate with life processes are mostly synthesized within living organisms under the catalysis of proteins called enzymes. The specificity of these catalysts make improbable reactions occur rapidly. In fact, little more than 150 years ago it was erroneously thought that only life forms could make "organic" compounds. The first organic compound synthesized in the laboratory was urea, by Wohler in 1828; a second organic compound, acetic acid, was synthesized by Kolbe in 1845. In one sense, present organisms may be viewed as living demonstrations of what chemical reactions are possible. Catalysts only change the rate of a chemical reaction; they do not make anything happen which would not have occurred (albeit more slowly) in their absence. Every compound found in a living organism thereby demonstrates the finite probability of its formation by natural chemical processes.

Synthetic reactions, however, do require the input of energy. The forms of energy available on the primitive earth to trigger chemical reactions were primarily various types of radiation (Table 1). The major source was probably the intense UV component of radiation from the sun. Although our contemporary atmosphere screens the earth's surface from most of the solar UV radiation, the primordial atmosphere was essentially transparent to the solar UV output. Additional sources of energy were lightning, ionizing radiation and heat from various sources (Table 1). Organic synthesis from the components of the primitive reducing atmosphere has been demonstrated in the laboratory with nearly all these types of energy sources.

The classical chemical evolution experiment was the one carried out in 1953 at the University of Chicago by Stanley Miller and Harold Urey. In a spark discharge apparatus (Fig.2) a simulated prebiotic reducing atmosphere of ammonia, methane, water vapour and hydrogen was subjected to artificial lightning (electrical discharge). The initially clear liquid water in the spark discharge apparatus gradually darkened to deep red by the end of a week. Chemical analyses revealed that the waters of this man-made primordial atmosphere contained many organic compounds, including amino acids, urea and other substances important in the chemical scheme of life (Table 2). This experiment was a landmark in the study of chemical evolution, and rekindled interest in understanding the origin of life.

TABLE 1

Energy sources on the primordial earth which could be used to make and break chemical bonds[a]

Source of energy	$kcal/m^2/year$[b]
total solar radiation above 300 nm	2,600,000
solar UV radiation 200-300 nm[c]	34,000
solar UV radiation <200 nm[c]	410
corona discharge	30
natural radioactivity (based on the level of 4 billion years ago, to a depth of 1 km)	28
lightning	10
volcanic heat	1.4
solar wind[d]	1.9
cosmic radiation	0.014

[a] Data obtained from Dickerson, 1978.

[b] Energy in kilogram-calories available per square metre of the earth's surface per year. 1 kcal = 4186 J.

[c] Wavelengths of $\leq$300 nm are the most highly effective in promoting chemical reactions. For the simple molecules in the atmosphere of the primordial earth, only wavelengths of $\leq$200 nm were sufficiently energetic to be absorbed by these molecules.

[d] Very little of this energy now reaches the earth's surface.

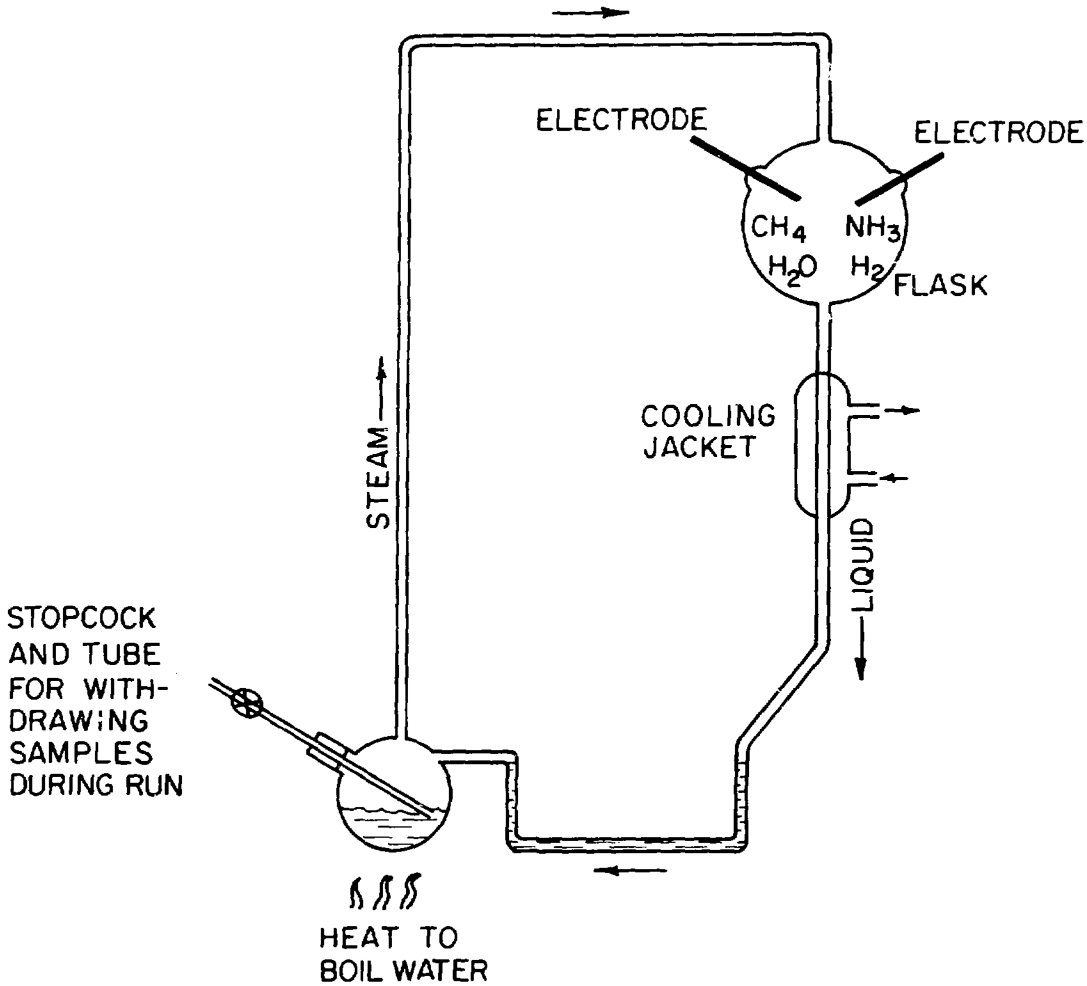


Fig.2. Representation of the Miller-Urey discharge apparatus. Organic compounds which form collect in the condensed water in the lower flask.

TABLE 2

Organic compounds obtained in the first run of the Miller-Urey spark discharge apparatus

Compound	μmoles formed[a]
glycine	630
alanine	340
sarcosine	50
β-alanine	150
α-aminobutyric acid	50
N-methylalanine	10
aspartic acid	4
glutamic acid	6
iminodiacetic acid	55
iminoaceticpropionic acid	15
formic acid	2330
acetic acid	152
propionic acid	126
glycolic acid	560
lactic acid	310
α-hydroxybutyric acid	50
succinic acid	38
urea	20
methylurea	15

[a] Originally the apparatus held 59,000 μmoles of carbon as methane gas. Approximately 15% was converted into the above compounds.

Other laboratories have since produced similar mixtures of the sorts of organic compounds which are regarded as necessary precursors of life by using other forms of energy, including ultraviolet light, electron bombardment (of energy selected to mimic that of ionizing radiation from the radioactive isotope potassium-40), gamma-rays or heat. In addition to the substances in Table 2, nucleic acid bases, sugars, nucleosides and nucleotides have all been formed under simulated primitive earth conditions. By subsequent reaction on various natural catalytic surfaces (mica, lava, etc.) the formation of the sorts of polymers found in biological systems has also been demonstrated. Given the availability of energy (mainly radiation of some sort), the starting materials and sufficient time (a billion years was available), organic synthesis was probably inevitable, the natural consequence of the interaction of energy and matter. In such simulation experiments, the application of energy produces material similar in appearance to the brownish coloured material in the clouds of Jupiter and Saturn.

These hydrogen-rich atmospheres are considered to have features similar to those postulated for the primitive earth. Chemical evolutionists hope that our space technology may soon let us analyse these planetary laboratories for prebiotic organic syntheses.

The putative "primordial soup" may have reached, by some estimates, a concentration for organic compounds of 0.1-1%; this could be further increased in localized areas due to various physical or chemical concentration processes, such as exist in tidal pools or in the mud of tidal flats. With the continuing input of energy, more and more complex molecules could arise. Random polymers (with some distant resemblance to the highly specific polymers utilized by life) can be produced from basic building blocks, for example by reaction on clay surfaces or at high temperatures such as might be supplied by lava from volcanic eruptions. Long chain hydrocarbons like those in living organisms have been formed in the absence of life. The acme of this chemical development was presumably the origin of a state of organization which could use material from the environment to repair, maintain, and replicate itself - in a word, life.

It is not so remarkable that the chemical compounds formed in the above experiments are similar to those formed by living organisms, if we bear in mind that such compounds anteceded the origin of life. If these are viewed as the molecular constituents available to primordial organisms, their chemical identity would of necessity be imposed upon that of living matter.

Organic substances similar to those formed in the preceding laboratory experiments have also come to our planet from outer space. About 3% of the meteorites which have been collected are classified as *carbonaceous chondrites*; they contain appreciable amounts of free carbon and other carbonaceous material. A fusion crust protects the core of the meteorite during its fiery passage through the atmosphere. The organic material in the core is regarded as clearly of extra-terrestrial origin and consists largely of hydrocarbons of composition similar to that in ancient terrestrial sediments and crude petroleum. Some people tended to regard these compounds as evidence for life in space; however, to say that a compound resulted from biogenic activity demands something more than merely its identification as a complex organic molecule. Most scientists believe that these compounds were formed by processes similar to those operating on the primeval earth and that the chondrite is representative of the dust from the primitive solar nebula which aggregated to form the solar system. The main significance of the presence of these hydrocarbons in carbonaceous chondrites is to show that complex materials can be produced in substantial amounts on a primitive micro-planet and can survive for long periods of time.

A wide variety of additional organic compounds, including amino acids, have been found in other meteorites. In many cases, these resulted from terrestrial contamination and/or handling. A number of lines of evidence, however, support the view that some of these sorts of organic compounds did arise by "chemical evolution" in a meteoritic extra-terrestrial laboratory. For example: (i) meteorites contain the "unnatural" optical isomer as well as the usual one (i.e. the one commonly used by living organisms) for organic substances with optical activity; chemical reactions outside living systems usually give such a mixture; and (ii) unusual amino acids, not encountered in living organisms but commonly formed in prebiotic synthesis experiments, have been identified. It seems therefore likely that organic synthesis in the absence of life is a cosmic event.

THE FIRST APPEARANCE OF LIFE

The spontaneous generation of the first successful living organism on earth may have been an event that happened once, and only once. Organic compounds which were formed in a prebiotic environment would persist because, unlike today, there would be no oxidation (since there was little or no free oxygen) and no decay (i.e. no attack by living organisms, the prime agency of decay, since there was no life). Once life arose, it might itself have prevented subsequent independent origins of life, because its processes might have altered the conditions that led to the original appearance of life.

Any living organism is an incredibly complex assembly of intricate organic molecules, the activity of which is coordinated in such a fashion that the organism can incorporate relatively simple nutrient materials from its environment, grow, maintain and reproduce itself. We do not know how this first division of the living from the non-living occurred. It has not yet been reproduced in the laboratory. But we might also recall that our understanding of natural processes has increased a great deal since the time when it was believed that no organic molecule could be synthesized in a test tube, and the formation of life in the laboratory should not be dismissed as forever beyond the realm of possibility.

What was the nature of this first form of life? It was likely microscopic in size and single-celled in structure. It probably arose in a localized area of the sea, where organic compounds (food and precursors) had accumulated, and where it would be shielded from the harmful far ultraviolet radiation. The elemental composition of life forms is quite different from that of the earth; for example, the relative concentration of carbon in most living organisms is roughly 100 times greater than that of the earth taken as a whole. The first forms of life may therefore have required concentration of precursors in tidal pools or estuaries, or within "droplets" of membrane formed from organic materials. But this separation of the living from the non-living did occur; the proof, one might say, is with us today.

The Russian biochemist, A.I. Oparin, who is regarded as the father of origin-of-life biochemistry, has studied the spontaneous aggregation of mixtures of various types of organic polymers into "coacervate droplets", which each consist of a membrane enclosing a droplet of the medium in which it was formed. One way to stabilize these droplets is to give them a primitive kind of metabolism. Coacervate droplet experiments mimicking energy metabolism, growth and division, respiration, photosynthesis, and biosynthetic reactions have been carried out. These experiments do not demonstrate life, but some of them get quite close to it. They demonstrate the extent to which life-like behaviour is grounded in physical and chemical phenomena. In the primordial sea, these various types of droplets might compete for material; those with the more favourable chemistries would be more stable and form an increasing proportion of the total. What they lack is a way of ensuring that the biochemical abilities of a parent droplet get transferred to a daughter droplet.

It is of interest to note that living organisms on earth currently utilize almost exclusively the L-isomer of the optically active amino acids, although in abiotic synthesis of amino acids from inorganic chemicals, equal amounts of both D- and L-isomers are found; both isomers are similarly present in some meteorites. Structurally ordered protein molecules such as found in living organisms can be formed from a sequence either of D- or of L-amino acids, but not from a random mixture of both isomers. The primitive selection by life of L-isomers rather than D- isomers may have been nothing more than a "cosmic throw of the dice" - a matter of 50% chance that the first successful organism used proteins consisting of L-amino acids rather than proteins consisting of D-amino acids.

FOSSIL RECORDS

Some of the early evolutionary steps can be seen directly in recently discovered micro-fossil records.

Most Precambrian sediments have been so altered by heat and pressure that fossils have been obliterated. A few regions have escaped such metamorphosing, however; there are to date three known fossil-bearing Precambrian areas which show evidence of key events in organic evolution:

(1) The first is the Fig Tree cherts in Swaziland; these have an age of 3.2 billion years. Thin sections have revealed micro-fossils of rod-shaped organisms comparable to modern bacteria in both shape and size; these were named *Eobacterium* (*eo* is the Greek word for "dawn"). Evidence of spheroid micro-organisms was also found. Recently it has been reported that certain rocks in Australia also contain fossils of other micro-organisms; these have tentatively been dated as 3.6 billion years old. It appears therefore that several distinct organisms inhabited an aquatic environment over three billion years ago.

(2) Cherts in the Gunflint formation on the northern shore of Lake Superior contain micro-fossils deposited in an aquatic environment and preserved in excellent three-dimensional detail by infusion of silica. The formations in which they were found have been dated at two billion years. A diversity of primitive plant forms was found among these micro-fossils. Evidence that these organisms were indeed photosynthetic is derived from the ratios of stable carbon isotopes (^{12}C and ^{13}C) in these fossils. The Gunflint organisms are therefore representative of the evolutionary changes that brought about our present oxygen-rich atmosphere.

(3) The Bitter Springs cherts in Australia are about one billion years old. They include fossils of plants that are eukaryotic, which are organisms capable of sexual reproduction.

The reasons why these three stages were key steps in the evolution of life will be explained when we consider energy metabolism, the development of the protective ozone layer, and the advantages of sexual reproduction.

Then, about 500 million years ago, the rate of evolution of different life forms began to accelerate rapidly; fossil records indicate that the Paleozoic seas were swarming with highly differentiated aquatic plants and animals. The human species is of course a relatively late arrival on the scene and probably arose only a few million years ago.

The period of five billion years since the earth's formation is an exceedingly long time in terms of a human life. To place these time scales into some kind of perspective which is more easily understood, we might think of the history of the earth as compressed into one year of our time-scale. In these terms, the earth would have been assembled into something like its present form during the first week(s) of January. Abiotic chemical synthesis, similar to that which can be simulated in the laboratory, occurred during the next three months. The first visible fossil record of living organisms dates from the end of March. Photosynthetic organisms appeared towards the end of July. Primitive organisms capable of sexual reproduction were present by mid-October. A wide variety of highly differentiated plants and animals start to appear in the fossils dating from the latter part of November. The first animal that distinctly resembles contemporary humans appeared late in the afternoon of December 31, while Columbus' first voyage would, in these terms, have occurred about three seconds ago.

SOURCES OF ENERGY FOR EVOLUTION

In order for a primal organism to obtain the energy essential for growth and reproduction, it would have to feed upon the constituents of the "organic soup" formed by over one billion years of chemical evolution. This is the same organic soup in which it was itself formed. This mode of life is called heterotrophic; an organism which cannot manufacture its own building blocks must rely on external sources of these materials, and in order to obtain the energy to assemble these building blocks into a replica of itself (that is, to grow and reproduce, a fundamental requirement of life), the organism must break down other organic materials in which energy has been accumulated. Since little or no free oxygen was available, this process must have been anaerobic. A number of mechanisms for this type of process exist in present-day living organisms. The most familiar example, and the one we shall use for illustrating energy relationships, is the fermentation of sugar by yeast. The initial steps in this ancient process are still utilized by humans, in fact, as part of our biological heritage.

$$\underset{\text{sugar}}{C_6H_{12}O_6} \xrightarrow{\text{fermentation}} 2\ CO_2 + 2\ \underset{\text{ethanol}}{CH_3CH_2OH} + 20\ \text{kcal}$$

To the cell which needs energy to stay alive, the carbon dioxide and ethanol are waste products. The production of useable energy from the break-down process is what is important, since it may be utilized for biosynthetic reactions. However, this is an inefficient way of utilizing this foodstuff; only a small portion of the total energy available in the sugar is released. The extent to which an organism could grow and divide under these circumstances is limited. Furthermore, an organism of this kind is "consuming its heritage", and its descendants would eventually run out of organic compounds. This life-style, since it relies on compounds formed abiotically (primarily by radiation), would be limited by the relatively low rate of production of organic molecules by such processes. How could life expand beyond such limits?

The next major step in the evolution of life appears to have been the necessary invention of a way for cells to capture solar energy directly in order to make their foodstuffs; this was the development of the process of photosynthesis.

Again, a number of mechanisms for this type of process have been developed by living organisms. Photosynthetic processes probably first arose in algae in the oceans; the photosynthetic pigment in an ancient phylum, blue-green algae, is particularly adapted for maximum utilization of the particular wave-lengths which penetrate sea water (Fig.1). The most successful mechanism, and that with which we are most familiar, involves photosynthesis in green plants with chlorophyll as the trap for radiation energy from the sun. In photosynthesis, sugar is synthesized from carbon dioxide and water by the reaction:

$$6\ CO_2 + 6\ H_2O + \underset{\substack{700\ \text{kcal} \\ \text{radiation energy}}}{\text{sunlight}} \xrightarrow{\text{photosynthesis}} C_6H_{12}O_6 + 6O_2$$

The carbon source for fixation might be the waste carbon dioxide from fermentation. With this chlorophyll-based process, radiation from the sun was tapped directly, and the slow, intermediate, abiotic formation of energy-yielding compounds by such radiation was by-passed. These organisms could now live on radiation energy at first hand. The photosynthetic process freed these organisms (and of course others which could feed upon them) from relying on the accumulated organic material, and allowed life to expand beyond the limits of such accumulated matter.

In its turn, photosynthesis gave rise to other profound consequences: for example, free (molecular) oxygen is released as a by-product of the photosynthetic process. With time, oxygen produced initially in the seas by algal photosynthesis entered the atmosphere in progressively increasing amounts. The free oxygen in our present atmosphere is there mainly because life did evolve this particular process of photosynthesis. This free oxygen led to formation of the ozone layer, which shielded the land surface from the antibiotic far UV component of the radiation emitted from the sun. This enabled living organisms to move from an aquatic environment (since water absorbs UV radiation effectively; cf. Fig.1) to a terrestrial habitat.

Recent concerns about the use of freon sprays and high-flying supersonic jets, whether justified or not, are in fact based on the possibility that these activities might reduce the protective ozone shield.

But the release of oxygen liberated organisms in another sense. The anaerobic fermentation process is a very inefficient method for an organism to obtain energy. With free oxygen available, a new way of acquiring energy could be invented.

This is the process of aerobic metabolism or respiration, wherein oxygen is used as the terminal electron acceptor in the stepwise oxidation of sugar:

$$C_6H_{12}O_6 + 6O_2 \xrightarrow{\text{respiration}} 6\ CO_2 + 6\ H_2O + 700\ \text{kcal}$$

By complete combustion to fully oxidized end-products, the maximum possible amount of energy may be extracted from the foodstuff, The energy yield in respiration is 35 times as much per mole of sugar as is obtained from fermentaton. (Reduced compounds are "energy-rich". Oxidation reactions release energy; the greater the oxidation state of the products, the greater the amount of energy that can be released.)

Nature seldom if ever puts "all its eggs in one basket". Evolutionary processes have made other attempts at more efficient combustion of food substrates. These also involved complete combustion but used other oxidizing substances, such as sulfur, as ultimate electron acceptor. A combustion process using an omnipresent gas offers a number of advantages, and certainly it was organisms using oxygen that progressed further up the evolutionary ladder.

Life on this planet had now been brought to some semblance of balance with respect to organic components and energy metabolism. The two equations for photosynthesis and oxidative respiration represent a balanced cycle wherein electromagnetic energy radiated from the sun is converted into chemically bound energy which living organisms use for their various purposes. Ultimately all our foodstuffs, directly or indirectly, depend on radiant energy from the sun. So does our oxygen. Solar radiation drives this cycle (Fig.3) by providing a source of energy which can be captured by pigments in photosynthetic organisms and which is needed to convert oxidized (energy-poor) compounds into reduced (energy-rich) foodstuffs. The subsequent combustion or oxidation of these foods yields energy which can be coupled with the biosynthetic reactions necessary for organisms to grow and reproduce. Photosynthetic organisms must "fix" enough energy for their own use and, in the final analysis, for the use of all non-photosynthetic organisms. The simple net equation obtained from the cycle of Fig.3 reveals that the biosynthetic processes of life are driven by radiation energy from the sun. The incredible diversity of life forms carrying out each of the two basic reactions of Fig 3 imparts considerable flexibility to this cycle.

What we have seen in all this is how life processes were dictated by **chemical and physical** laws. Life is characterized by a remarkable adaptability to the available chemistry.

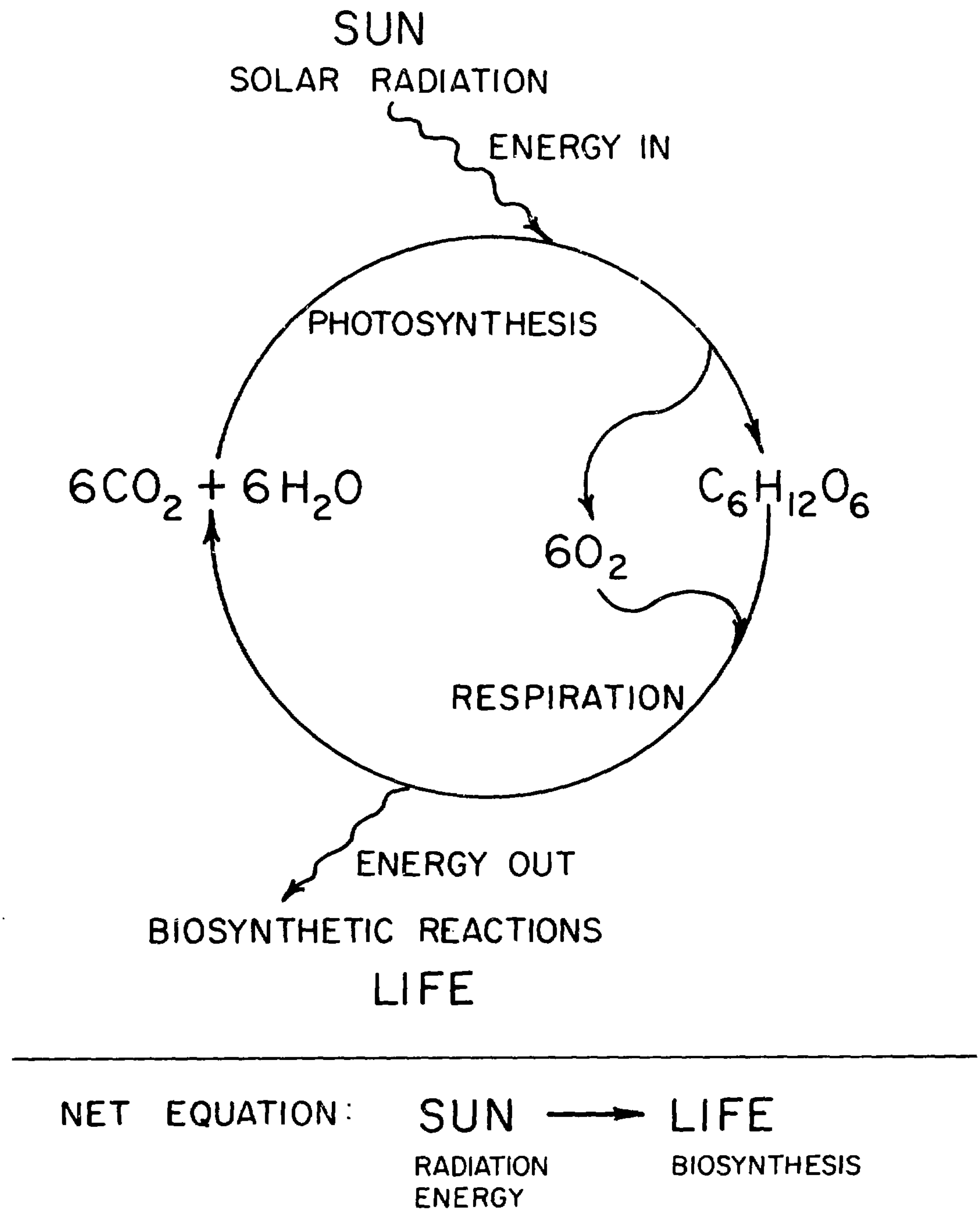


Fig.3. Photosynthesis and respiration form a closed system whereby radiant energy from the sun is converted to a form of energy which can be coupled to life processes.

VISION

Radiation from the sun also allows vision (i.e. detection of objects in our environment by means of radiant energy reflected from these objects). The wave-lengths used for vision are 400-700 nm; this also happens to be the range where the sun's output peaks. Image-forming eyes are found in only three phyla: arthropods (insects, spiders, crabs), molluscs (octopus, squid), and vertebrates (mammals, birds, fish, etc.). The three kinds of eyes differ in anatomical features, embryological development and evolutionary origin.

When the chemistry of the visual process is examined in these three completely independent developments of eyes, the remarkable finding is that the chemistry is essentially identical. In all three, retinene (the aldehyde form of vitamin A) is the pigment which absorbs the light that stimulates vision. Vitamin A cannot be made *de novo* by animals; it is derived from plant carotenoids obtained in the animal's diet. The structure of vitamin A is basically that of one-half the β-carotene molecule. Radiation energy from the sun therefore provides not only the wavelengths for excitation of the visual process, but also, by photosynthesis in plants, the essential visual pigment itself.

The carotenoids, in fact, are also the pigments responsible for phototropism in plants. All photo-reception in living organisms therefore depends on carotenoids as the light-sensitive pigment(s). Carotenoids are highly conjugated systems of a type resulting from condensation reactions in chemical evolution experiments. It seems likely that this early biopolymer was selected and adapted by living organisms for the chemistry of all photo-reception purposes.

DARWINIAN EVOLUTION AND NATURAL SELECTION

A billion years or so after photosynthesis originated, the third major threshold in the evolution of life was crossed; this was the invention of the eukaryotic cell and sexual reproduction, with its potential for recombination and genetic diversity. It is this factor which was apparently responsible for the tremendous expansion of life forms, with its rich fossil record, over the last several hundred million years. Since the relative importance of this development is best explained in the context of Darwinian evolution, mutation and natural selection, we shall now consider these subjects and the involvement of radiation with them.

Darwin's theory of natural selection as the driving force of evolution envisaged the occurrence of random heritable variations among the individuals in a population; through natural selection, those that are advantageous tend to persist and expand, while those that are deleterious tend to disappear from the population. Although the concepts have grown more sophisticated over the past 120 years, the basic precepts are still accepted as correct by biologists. Indeed, the evolutionary process is readily studied in the laboratory and is reproduced daily on a small scale in research laboratories around the world.

It is convenient to think of evolution as having two steps: (a) The first is the production of heritable changes (i.e. genetic variation). This variability is continually arising, and therefore is random in the sense that it is unrelated to the current needs or life-styles of the organism. These processes result in a pool of genetic variability being present in a population. (b) The second step is natural selection: organisms "compete" with others in various niches. As the circumstances or environment change, one genetic constitution may confer a competitive advantage. This results in a reproductive advantage, and descendants of this particular genetic make-up will thus form an increasing proportion of the population of that species. The Darwinian fitness or biological success of an organism is measured by its ability to leave descendants, and by no other criterion. In a sense, natural selection "blindly" follows the need of the moment; it favours any variation which confers a competitive advantage.

Although mutations play a vital role in evolution, they are harmful as well as necessary. This may at first seem to be a serious objection against a theory which regards mutations as the mainspring of evolution. Yet, a pool of genetic variability is valuable to a species because only species with an ample supply of mutant genes are able to adapt to a new ecological niche or accommodate a changed environment. There is a cost of mutation, in reduced fitness of the population, and the individual organism pays the price. But the population benefits; it is mutation that makes gradual evolution of the species possible. Mutation might be regarded as the price a species pays for the privilege of evolving. In order to survive and adapt to changing conditions over a long period of time, each species must therefore strike a balance between a long-term advantage of genetic variability and the short-term advantage of a low mutation frequency. What we see as the spontaneous mutation rate may represent the balance a species strikes between these conflicting objectives.

The heritable variability necessary for evolution by natural selection arises by mutation and recombinational changes in the DNA-based genetic system, which will be described next.

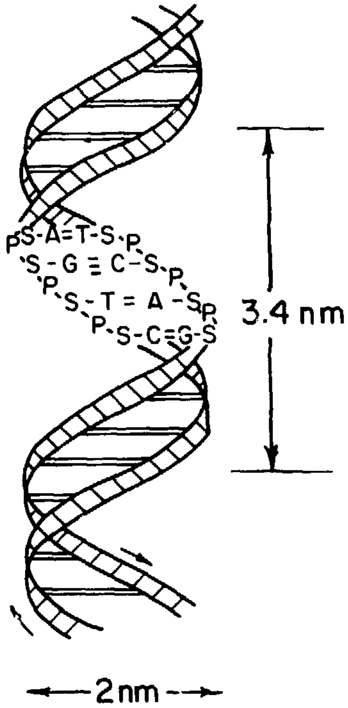
DNA, THE GENETIC MATERIAL

About three decades ago, biologists became aware that the hereditary information directing reproduction and all life processes is encoded in a long thread-like double-stranded (duplex) molecule called deoxyribonucleic acid, or DNA. The DNA molecule in a particular living organism represents a blueprint or coding tape for its construction and functioning. It stores all the genetic information that is passed from one generation to the next and in this manner ensures that the major characteristics of living things remain essentially constant over many generations.

The DNA molecule is a double helix (Fig.4); it consists of two strands of alternating sugar and phosphate moieties in a "backbone" wound around each other in the form of a spiral staircase. The "steps" in the centre of the spiral staircase consist of paired sets of one purine base (adenine or guanine) and one pyrimidine base (thymine or cytosine). The adenine in one strand always pairs with a thymine in the other; similarly guanine always pairs with cytosine. The base pairs are held together by hydrogen bonds which are individually weak but collectively quite strong. It is actually this sequence of bases along the length of the molecule which provides the coded information for the intricate chemical processes carried out by a living cell.

Because of the strict hydrogen-bonding base pairing, the two strands are complementary, much like a photographic negative and its positive print. Either is sufficient to dictate or specify the other. Given a sequence of part of one strand, the complementary sequence of its opposite strand may be easily written down. This redundancy forms the basis for both the normal accurate transmission of genetic information and for DNA repair.

DNA is an extremely long molecule even though it is barely visible in the electron microscope. The total amount of DNA in an individual human cell (itself about 10,000 nm in diameter) would represent a thread about 2 nm in diameter (Fig.4) and 2 billion nm (2m) in length. If all the DNA in the human body were stretched out and placed end to end, the total length would reach from the earth to the sun (250 million kilometres) and back about fifty times. This DNA from a single human cell totals nearly 10^{10} base pairs along its length; encoded in this material are a very large number of separate instructions for life processes. Even though the genetic code has only four letters (those of the four bases), it amply fulfills the requirements for an informational molecule. The number of different possible combinations of base pairs in the DNA of a single human cell is about $10^{6,000,000,000}$, immensely greater than the total number of atoms in



PURINE----PAIRS WITH----PYRIMIDINE

A ⟷ T

G ⟷ C

10 BASE PAIRS AND 3.4 nm
PER "TURN"

ALTERNATING SUGAR (S) AND PHOSPHATE (P) RESIDUES FORM THE BACKBONE; THE NUCLEIC ACID BASES PAIR BY HYDROGEN BONDING ACROSS THE LONG AXIS OF THE MOLECULE.

Fig.4. The double helix: DNA.

the solar system (about 10^{57}).

It is not known whether DNA formed an integral part of the first successful living organism, since this molecule leaves no fossils. The fossil record, however, indicates that chromosomal structures, much like the current structures in which DNA is organized in living organisms, existed one billion years ago, and the fact that blue-green algae appear to have existed for two billion years suggests that DNA has functioned as the carrier of genetic information for at least this long. Another informational macromolecule, ribonucleic acid (RNA), also exists in living organisms. Both RNA and DNA have properties suitable for a carrier of genetic information. Because RNA, in contrast to DNA, possesses two adjacent hydroxyl groups on its sugar residue, it is less stable than DNA and is, for example, much more readily degraded by alkali. Living organisms today utilize the more stable informational molecule, DNA, as a master copy or the permanent carrier of hereditary information while the less stable macromolecule, RNA, is utilized to make temporary intermediate copies of this information for actual use by the machinery of the cell. The absence of a hydroxyl group in the 2-position of the sugar residue in DNA also eliminates the possibility that the sugar-phosphate "backbone" of this macromolecule could involve phosphate esters of the 2-position; the latter structure is less suitable for the formation of a stable, double-stranded structure.

DNA REPLICATION

The basic unit of life is the cell. Micro-organisms usually occur as discrete and independent cells, each of which can grow and divide to form two daughter cells. More complex organisms such as humans consist of an assemblage of about 10^{13} cells, all coordinated to form a single living organism. This complex assembly itself arises from a single cell (the fertilized egg cell) through a process of many cell divisions. Not only is the cell division controlled by instructions in the DNA, but the DNA itself must be duplicated at each cell division.

When one cell grows and divides to form two "daughter" cells, each must receive an accurate replica of the genetic information if the characteristics of the progeny are to be similar to those of the parent cell. The means by which this is achieved is built into the DNA structure. For DNA duplication or replication, the two strands progressively separate; they may be regarded as "unzipping" at the weak hydrogen bonds (Fig.5). As they separate, each single strand can now serve as a template for formation of a new opposite strand.

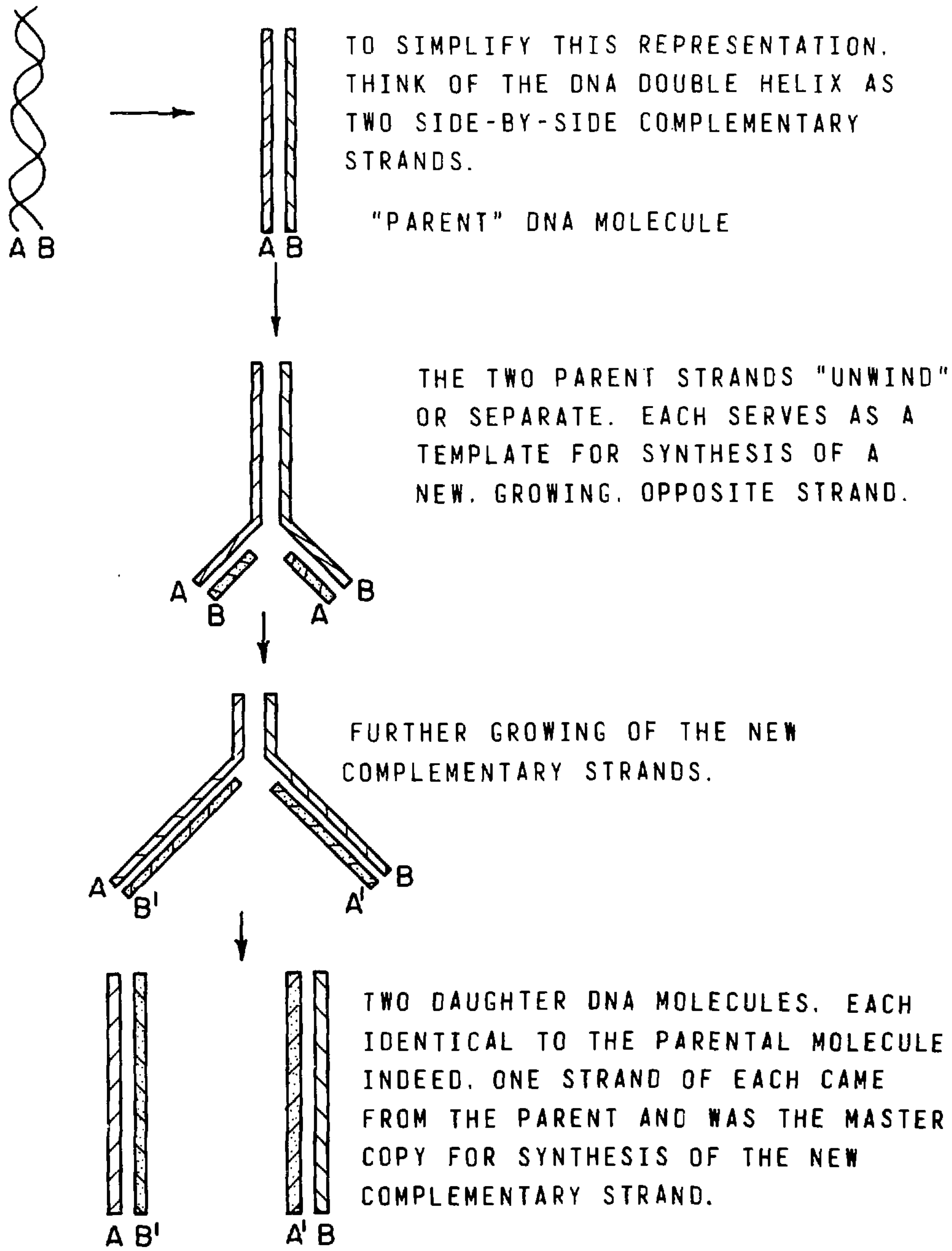


Fig.5. Representation of DNA replication, showing how the genetic information in one cell can be accurately duplicated in order to furnish one whole copy to each of two daughter cells.

This synthesis utilizes the specific base-pairing interactions to attract the correct building blocks from solution and links them together into a polymeric complementary strand. This complementarity rules assure the fidelity of replication. The result is two daughter DNA molecules, each apparently identical to the original in every aspect more than 99 times out of each 100 times that this replication process occurs. In a human cell with ~10^{10} base pairs, this implies an error frequency of less than once in 10^{12} times per base unit added.

THE FLOW OF GENETIC INFORMATION

In the provision of instructions for life processes, the genetic material (DNA) acts as a master copy. The DNA molecule is a linear sequence of functionally distinct groups of bases called *genes*; each gene codes for a particular product. The first step in using the DNA code is to make a copy of the base sequence of a portion of one strand of the DNA double helix in the form of a single (complementary) strand of "messenger" nucleic acid (Fig.6). This process is called *transcription* because the same language (a sequence of nucleic acid bases) is used to convey the genetic information; a different type of nucleic acid (ribonucleic acid or RNA) is used to keep this transcript or copy distinct from the copy made at replication. This messenger RNA goes to the protein synthetic apparatus (the ribosomes) where its bases are read in sets of three, the so-called triplet codon. Each set of three bases corresponds to a particular amino acid to be linked up in the protein which is eventually synthesized as end product (Fig.6). This process is called *translation* because the language has been changed, from a nucleic acid sequence to an amino acid sequence. For example, the sequence guanine-cytosine-cytosine in the original DNA is read off and copied in the messenger RNA as a complementary sequence; this expendable copy is then utilized by the synthetic machinery of the cell to specify the amino acid glycine at a given location in the protein that is being synthesized. These proteins are the functional machinery of the cell, and their actions determine in large part the characteristics of a cell.

Evolution depends largely on progressive substitution of one amino acid for another in a given protein. This may alter the characteristics of the protein, and make it less or better able to perform its function or assume a new function. A mutation at the molecular level therefore occurs first as an altered base in the genetic material, DNA, which will change the codon in messenger RNA and thence specify a different amino acid in a protein.

Since evolution is a gradual process, organisms which diverged recently are more likely to be similar to one another than are organisms which show a more distant ancestor. This obvious assumption is the basis for attempts to

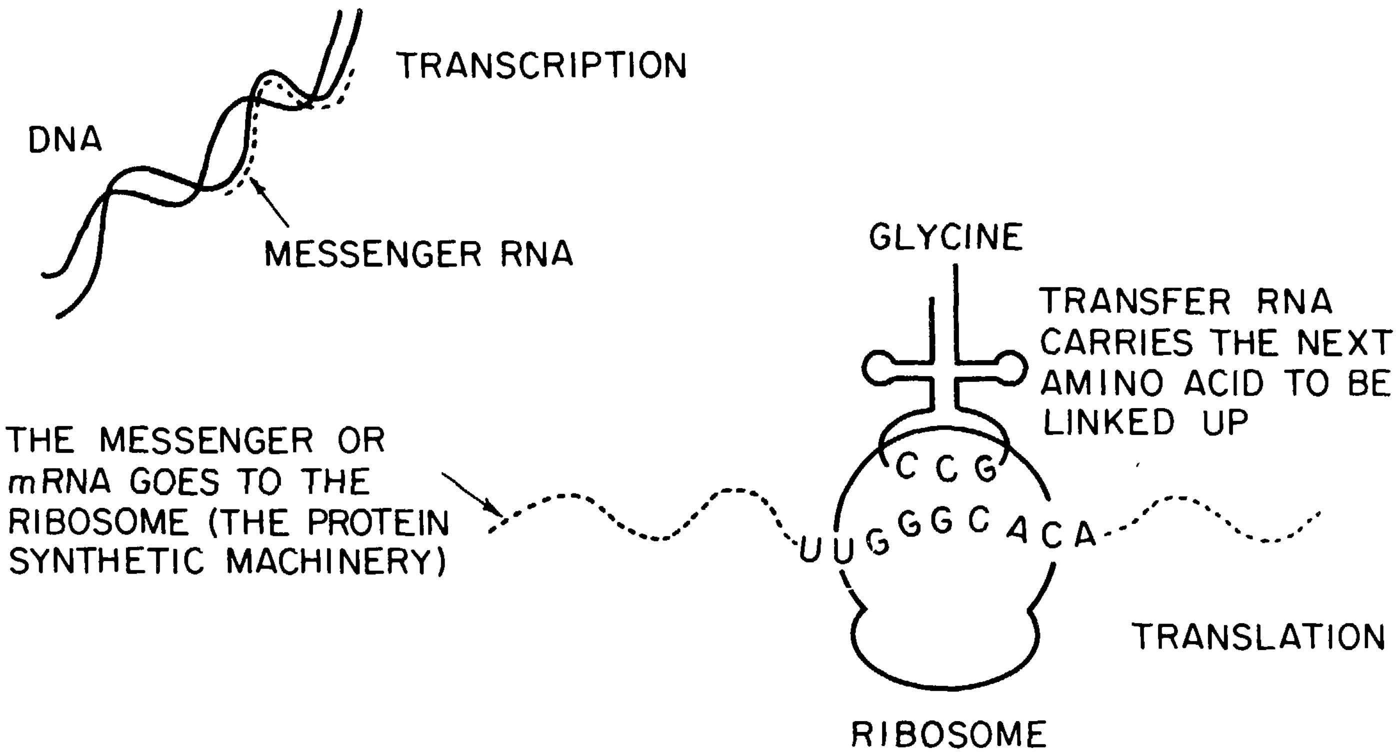


Fig.6. The flow of genetic information from DNA to messenger RNA to protein.

reconstruct evolutionary history by comparative studies of the anatomical features of organisms. This approach is difficult to apply to distantly related organisms. Modern molecular biology has furnished an elegant alternative, however. In one sense, DNA can be viewed as a living document since extant organisms carry a record of their antecedents within it. Since the amino acid sequence of a protein is a linear reflection of the sequence of bases in the gene coding for it, this principle has become a powerful tool for studying evolutionary history. If a protein which serves a particular function common to almost all organisms, such as that served by cytochrome c in the process of respiration, is studied in various species, it is found that the number of differences between any two cytochrome c species is approximately proportional to the length of time since the divergence of these species, as inferred from traditional sources like the fossil record. Phylogenies can be constructed exclusively on the molecular basis of these sequence differences, which have been described as "chemical footprints on the evolutionary trail". One interesting result which has emerged is that all sequences converge to a common ancestral type, suggesting one effective emergence, for example, of the particular catalyst known as cytochrome c, and, by inference, one effective emergence of life forms capable of aerobic metabolism (respiration).

In fact, the genetic code itself seems to be universal - all living organisms employ the same codon catalogue for translation. This also indicates that all present life forms may have originated in the past from a single cell line, which already possessed at that time the features of the code now regarded as universal. Possibly, a large number of sets of codon assignments, perhaps many equally good, were tested by evolution, involving a large number of organisms living under a wide range of circumstances. In these circumstances, to account for universality one has to postulate that some crucial event in the course of evolution caused all subsequent life to be derived from a particular cell line. This, for example, could have been the development of a superior translation apparatus, or similar internal occurrence. Since fundamental mutations of the type that change codon assignments are now usually lethal, the genetic code may have been locked in for all time according to the codon catalogue in this primordial cell.

MUTATION FROM DNA DAMAGE

Any damage to the genetic material, DNA, which affects the fidelity of replication or changes the pairing properties of a nucleic acid base, can give rise to heritable alterations. Furthermore, no chemical is totally inert, particularly in an oxygenated aqueous environment; DNA is a chemical, and is no

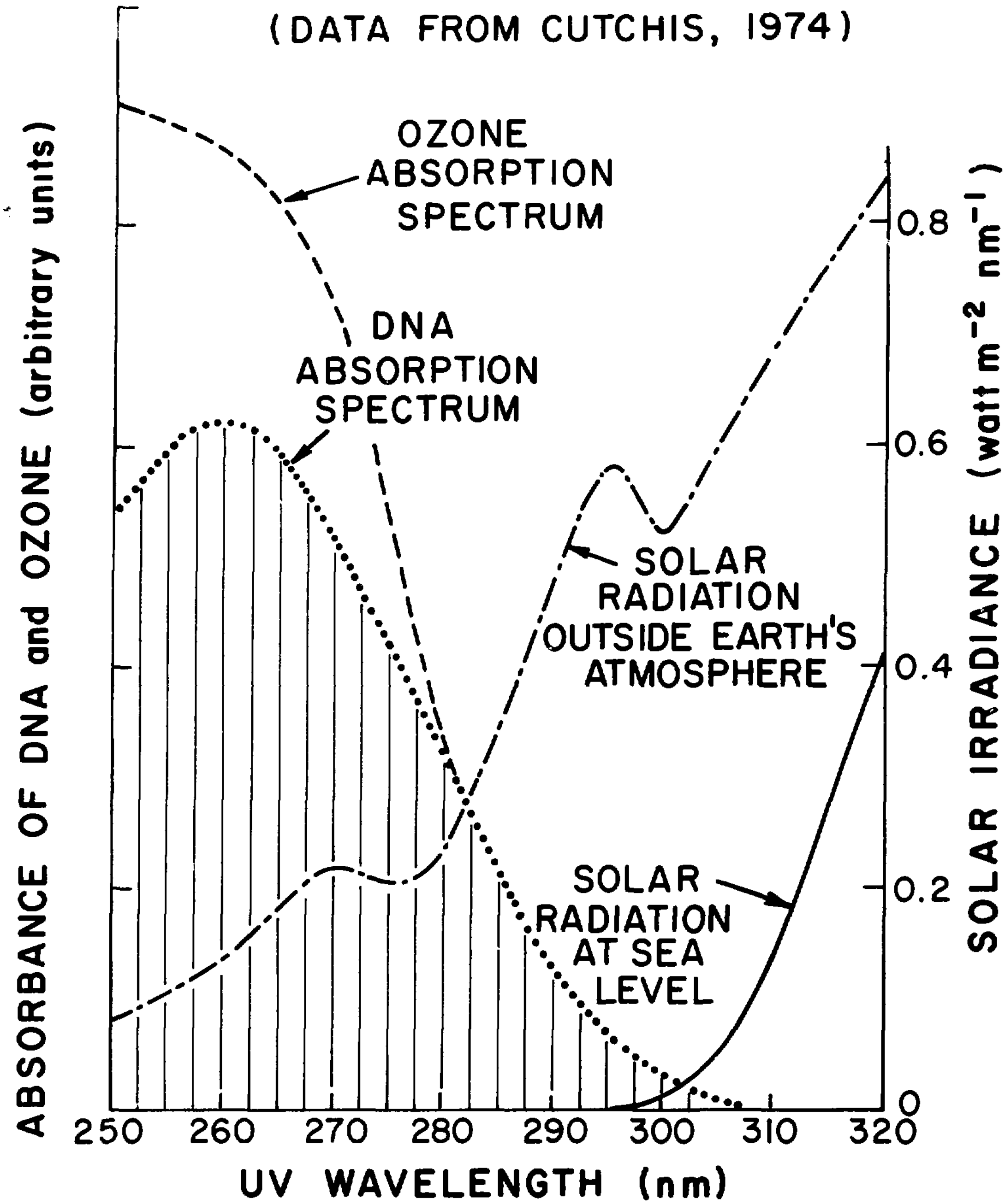


Fig.7. Solar radiation in the ultraviolet region below 290 nm would be efficiently absorbed by DNA and result in damage to DNA, but does not now reach the earth's surface because it is currently absorbed by ozone in the stratosphere. The DNA and ozone absorption spectra have been normalized to the same absorbance at 290 nm in this graph. Only a small residue of solar ultraviolet radiation, in the region between 295 and 320 nm, remains to affect the DNA of living organisms on the earth's surface.

exception to this rule. Therefore changes can arise spontaneously because of straightforward chemical alterations, as a result of absorption of energy from various radiations (causing molecular transitions), or by reaction with various chemicals in the environment. Table 3 gives an indication of the relative contribution expected from these various causes.

The ultraviolet component of solar radiation, which is strongly absorbed by nucleic acid bases, probably played the greatest role of any type of radiation in production of mutations. It is not certain how much of a contribution it made to the overall production of mutations, but it certainly would have played a much greater role in the past, before development of the ozone layer, than at present. The absorption spectrum of the protective ozone layer closely corresponds to that for nucleic acids (Fig.7).

If ionizing radiation has played any important role at all in evolution or the production of mutations, it is probably in those organisms such as man with a longer life cycle (Table 4); longer-lived organisms accumulate a larger total dose from the relatively low natural background radiation. Even for them, however, the proportion of total mutations which is attributable to the ionizing radiation exposure is quite low (Table 4). This suggests that a small increment in this level as a result of man's activities would not significantly increase the overall rate of production of new mutations.

It is difficult to say how much evolution owes to all radiation-induced versus spontaneously occurring mutations. Life forms were probably considerably more sensitive to mutation induction by various radiations in the past than they are today because: (i) DNA repair systems (see next section) were undoubtedly themselves an evolutionary development; (ii) simpler (especially single-celled) organisms would be less shielded and more vulnerable than multi-celled organisms to the most prominent source of damaging radiation, the UV component of sunlight; and (iii) a greater proportion of mutations were likely to be beneficial to a primitive organism than to a more adapted one. Mutation induction by UV radiation may therefore have made a significant contribution to the early evolution of life.

At present, detectable mutations are relatively rare events. The spontaneous mutation rate is thought to vary from about 0.6 to 6 new mutations per generation per thousand offspring for the organisms listed in Table 4. That is to say, more than 99% of the offspring do not contain a new mutation anywhere in their inherited information. Almost all, however, contain substantial amounts of genetic variability passed down from preceding generation; this will be discussed later.

TABLE 3

Approximate rates at which defects are introduced into the DNA of living cells

Cause of defect	Defects induced per cell per hour[a]	
	Bacterial cell (*E. coli*)	Human cell
Natural background of ionizing radiation (0.1 rem/year)	0.0000003	0.0003[b]
Spontaneous degradation	0.6	600[c]
Bright noon sunlight	2 thousand	2 million[d]

[a] A human cell contains approximately 1,000 times as much DNA as a typical bacterial cell, e.g. *Escherichia coli*; these two species span a range in which most other types of cells are included.

[b] These values are extrapolated from measurements in human cells at much higher radiation doses.

[c] These values are extrapolated from measured values with isolated viral DNA.

[d] These values were measured in unprotected human cells by Trosko (1970); minor corrections were introduced for formation of pyrimidine dimers using the data of Carrier and Regan (1980). Values calculated in an earlier document (Myers, 1977) are an order of magnitude lower because they allow for shielding of cells in unpigmented human skin by the superficial corneal layer of the skin; further shielding is provided by protective dark pigments in some types of skin.

TABLE 4

Contribution of the background ionizing radiation to total spontaneous mutation rate, in organisms with different generation times

Organism	Approximate generation time	Ratio of mutations that are caused by ionizing radiation from all natural sources over total spontaneous mutations
Yeast	2 hours	1/10,000,000
Wasp	14 days	1/10,000
Mouse	4 months	1/2,000
Human	30 years	1/30

DNA REPAIR SYSTEMS

Organisms, to protect themselves from DNA damage caused by exogenous agents and spontaneous chemical events, have evolved systems to assure the fidelity of transmission of their genetic information and to maintain its integrity. The genetic code, although exposed to various types of damaging events, is relatively stable at present; this is now recognized as due to the presence of active DNA repair systems. These DNA repair mechanisms have been found in all living cells which have been examined. Because of their existence, most of the initial damage caused to DNA by ionizing radiation, ultraviolet radiation, or spontaneous chemical alterations is eventually removed from DNA and therefore is without consequence. What we are concerned with, then, is not the initial damage induced but rather the amount of damage remaining after these DNA repair systems have acted.

Three basic DNA repair systems have been distinguished (Fig.8):

(a) *Photoreactivation* involves a single protein (the photoreactivating enzyme or photolyase) which captures the energy of visible light and utilizes it to correct one of the most common types of damage (pyrimidine dimers) produced in DNA by ultraviolet radiation. The light energy is used to monomerize the dimer *in situ*. This repair process is distinct from the following ones in that it does not depend on template direction from the opposite strand. This system has been found in many lower organisms but may not be significant in humans and other mammals.

(b) The *excision repair* system recognizes an alteration or damaged site in a strand, perhaps because the resultant lack of pairing creates a localized structural distortion or partially single-stranded region; this mechanism involves cutting out a portion of this strand including the damage. However, no genetic information has been lost; the complementary sequence in the intact opposite strand can now serve as template to direct resynthesis of the gap or excised portion with new, good material. In excision repair, then, a portion of one strand serves to direct repair of the corresponding portion of its partner strand, just as in DNA replication the base sequence in one whole strand can serve to direct the synthesis of an entire new opposite strand. The excision repair system involves the sequential action of at least four distinct enzymes (Fig.8), and a variety of enzymes seems to be present in cells to recognize particular types of damage to DNA and perform the initial incision.

(c) *Recombinational repair* must be invoked in those rarer cases where damage occurs in each of the two strands in a region essentially opposite each other. It was once thought that such double-strand or coincident lesions could not be repaired, since the template or pairing properties are altered in both strands. We now know that double-strand lesions are amenable to repair. In organisms

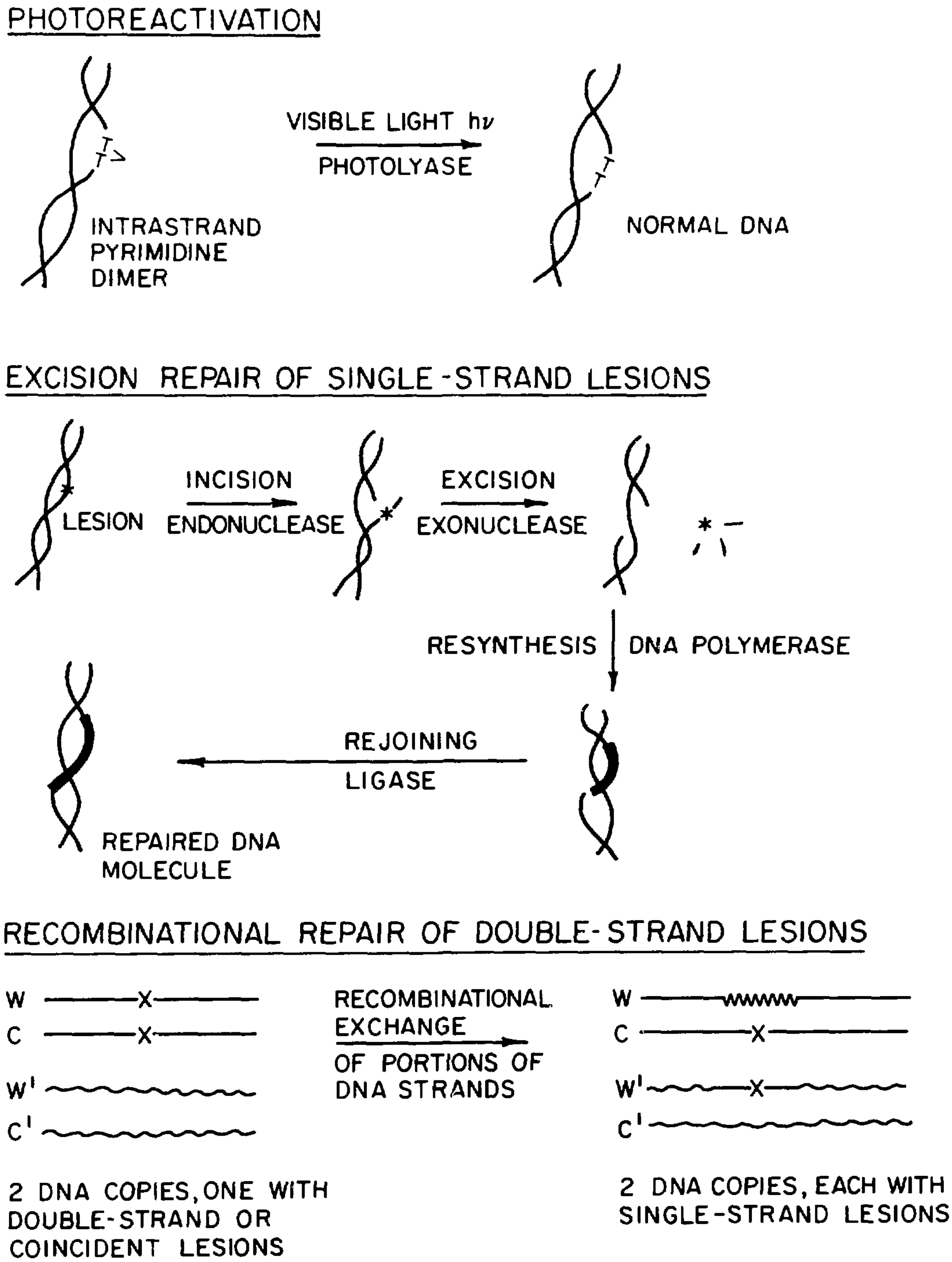


Fig.8. The principles of the three major DNA repair mechanisms. In the illustration for recombinational repair, the two different strands of the double helix are designated W and C (in honour of James Watson and Francis Crick, who elucidated the DNA structure), in order to distinguish them. Since the two molecules involved in recombinational exchange are homologous or "sisters", a W strand from one duplex molecule can pair with the corresponding region of either of the C-type strands.

which have two complete copies of a particular DNA molecule, the *recombinational repair* system permits the cell to exchange information between the two copies of DNA molecules and to utilize the second DNA molecule in repair of coincident damage in the first DNA copy. By recombinational exchange over a portion of the DNA, the original double strand damage is in essence converted to two instances of single strand damage. The damage has really been rearranged, but in so doing the template function necessary to direct subsequent excision repair has thereby been re-established.

Most sexually reproducing species are diploid; they contain at least two such complete copies of the genetic material. (As will be shown later, this has importance for storing genetic variability as well as for repair.) Haploid organisms, which contain one complement of genetic information, also have two copies for a portion of their cell cycle, when they have replicated their DNA preparatory to division into two daughter cells (each containing one copy). The importance of this recombinational repair process has been clearly demonstrated in certain such haploid organisms, where cells which have replicated their DNA prior to division (G2 phase of the cell cycle) are vastly more radiation-resistant and repair-proficient than cells which have not yet duplicated their DNA (G1 phase)(Fig.9).

Since the instructions for synthesis of the enzymes involved in these DNA repair processes are themselves encoded in genes in the DNA, they are themselves subject to mutation, evolution, and natural selection of their relative efficacy. Hereditary defects in those genes coding for such DNA repair activities can give rise to radiation-sensitive mutants which are inactivated to a greater extent than normal by a given dose of radiation. Such mutants are very useful in studying repair systems and the consequences of repair deficiency.

EVOLUTIONARY JUMPS

Most evolution is thought to be a slow step-by-step process compounded of minor changes at each step. Yet at particular times in the fossil record, there seem to be abrupt changes - new species seem to leap out. How do such "jumps" in evolutionary history occur? One of the major factors involved may be increases in the amount of DNA. Generally, the more complex and higher ranked species do in fact have much more DNA than lower species.

A particular gene gives a particular product with a particular function. Since (as we have mentioned) this gene is already the result of an age-old evolutionary process, it is highly adapted to its purpose, and the

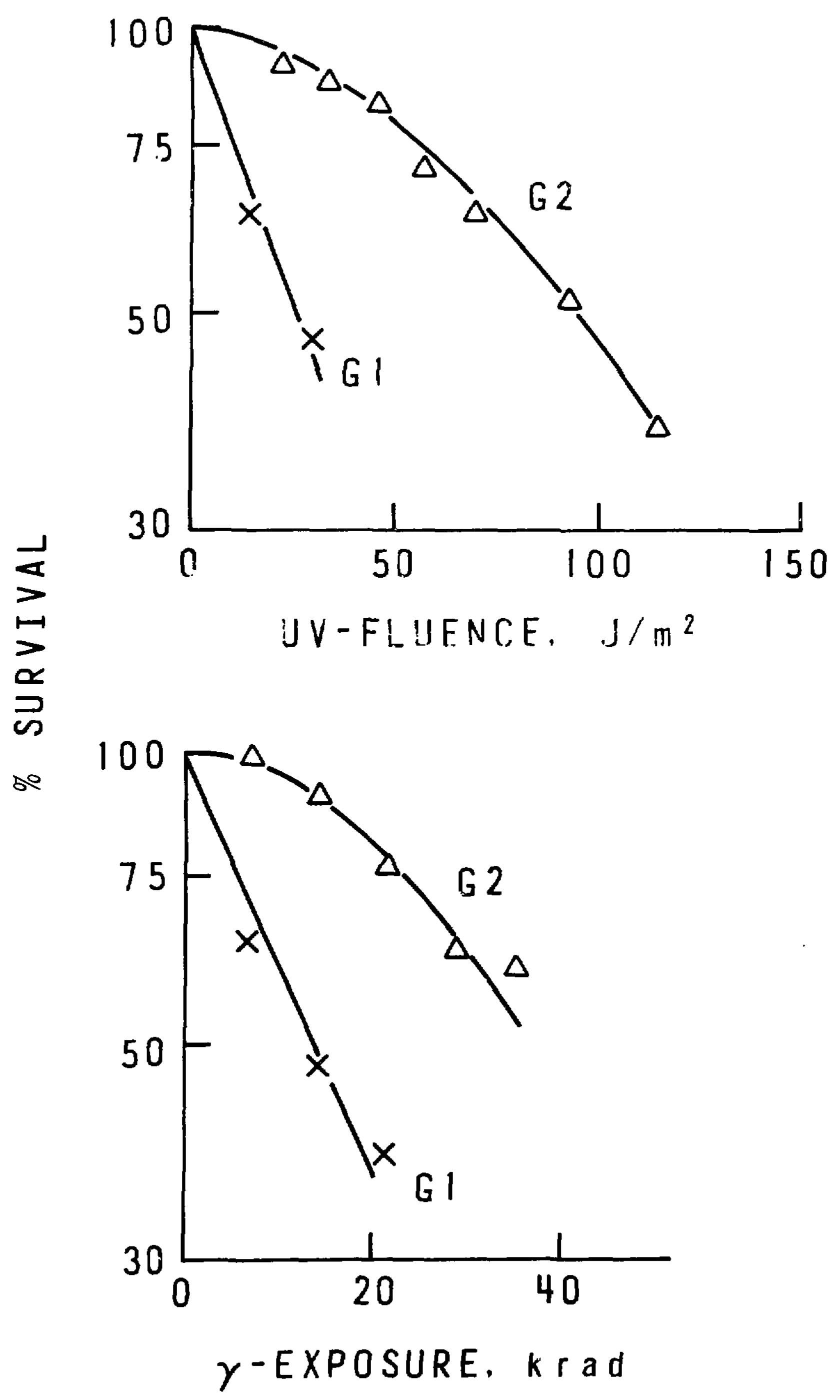


Fig.9. Relative UV- resistance (upper graph) and γ-resistance (lower graph) of cells of the yeast *Schizosaccharomyces pombe* which contain either one copy (G1) or two copies (G2) of the genetic information. Cells which contain two copies can perform recombinational repair while cells with only one copy cannot. 1 krad = 10 Gy.

same is likely true of most of the other genes in this organism. The existing gene functions are therefore subject to strong evolutionary constraints - that is, a change in the genetic information will probably be detrimental to the organism. Evolutionary jumps may therefore require increase in the amount of genetic material. This can occur by duplication of segments of DNA, of a whole chromosome, or of the entire genome. In higher organisms, the entire genome is duplicated in the form of paired or sister chromosomes; moreover, each of the paired chromosomes may contain multiple copies (some active, some inactive) of a given gene. Thus, although the measured amount of DNA in a human cell is 1,000 times greater than that in a bacterial cell (see Table 3), the number of genes is thought to be only 10 to 50 times greater. Most of the DNA in a human cell represents either non-functional or duplicate copies of functional genetic material. This has an important consequence: in the duplicated material, the DNA in non-functional or duplicated copies is freed from its essential role related to survival of the organism and can evolve independently a new function, since the other copy can retain the original function. Gene duplication thus facilitates creation of new functions and eventually new species.

Another sort of evolutionary jump should be mentioned; this is extinction. Extinction may be considered to be an evolutionary jump resulting in the removal either of "dead-ends" or of organisms which became so specialized that they could not adapt when the environment changed. The evolutionary fossil record, in fact, indicates that the overwhelmingly probable future for any complex species is extinction. The best known example of this process is probably the extinction of a wide variety of dinosaurs at tne end of the Mesozoic era some 60 million years ago. Although many of the more primitive species of living organisms appear to have survived for about a billion years, it has been estimated that 98% of present vertebrate families (e.g. animals,reptiles, fish and birds) owe their origin to eight particular Mesozoic organisms.

SEXUAL REPRODUCTION

The importance of sexual reproduction in evolution lies in its ability to provide genetic variability (which is the key to evolutionary progress) in a new way, distinct from mutation. The success of sexual reproduction in this endeavour is evidenced by the level of development, adaptiveness and remarkable diversity of living organisms which have used this route. The principles involved can best be appreciated by contrasting asexual with sexual reproduction.

In asexual organisms, each cell generally has a single DNA molecule or chromosome. Consider the situation if a mutation A should arise in one daughter cell and a different mutation B, in the other daughter cell line, and both mutations are advantageous (Fig.10). These mutations are relatively rare events and arise independently with a very low probability (say 10^{-8} per cell per generation). The first cell line would have to wait for mutation B to arise independently in its line of descent in order to acquire

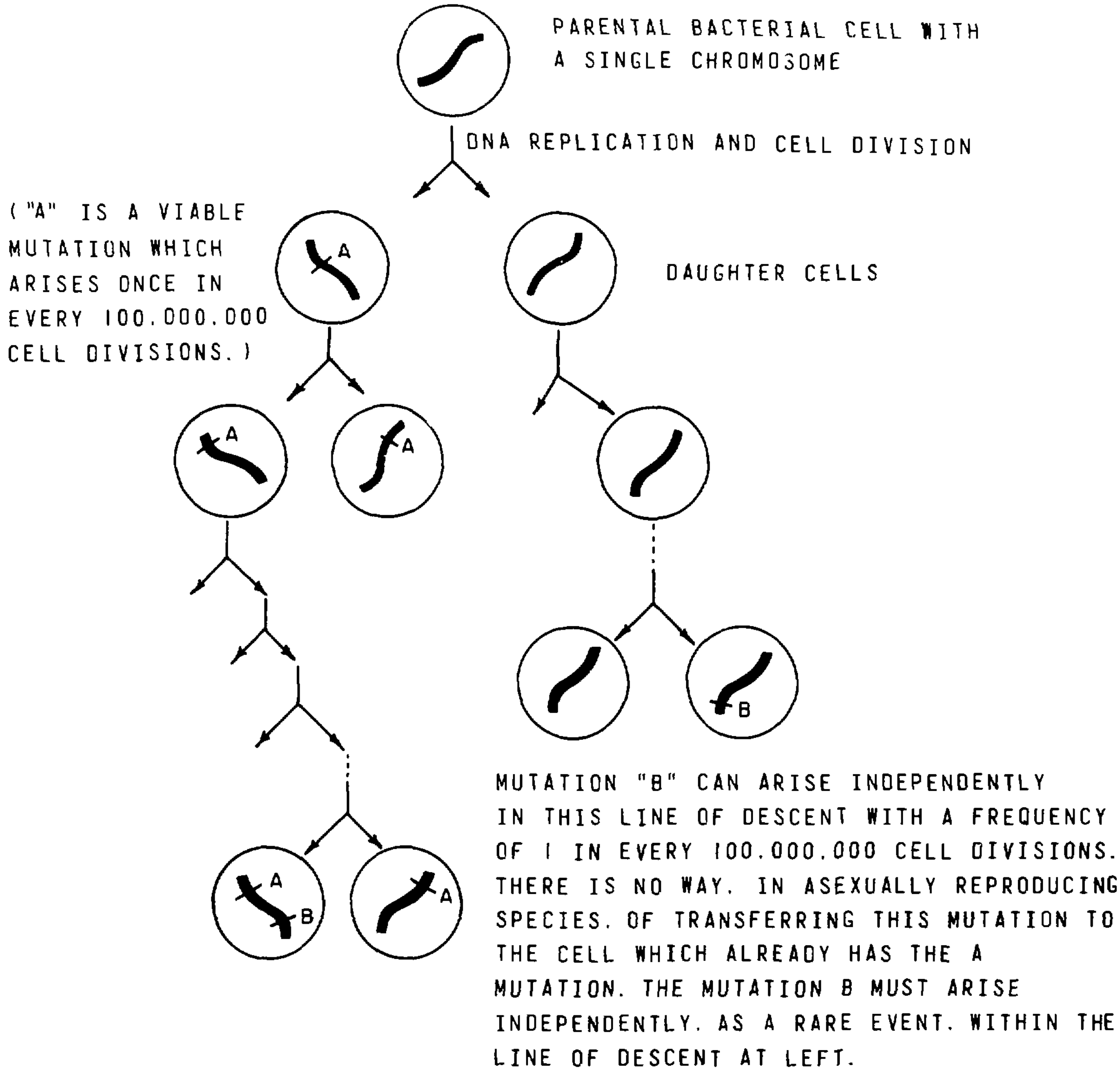


Fig.10 In species which reproduce asexually, evolution depends on newly occurring mutations to provide the necessary genetic variability.

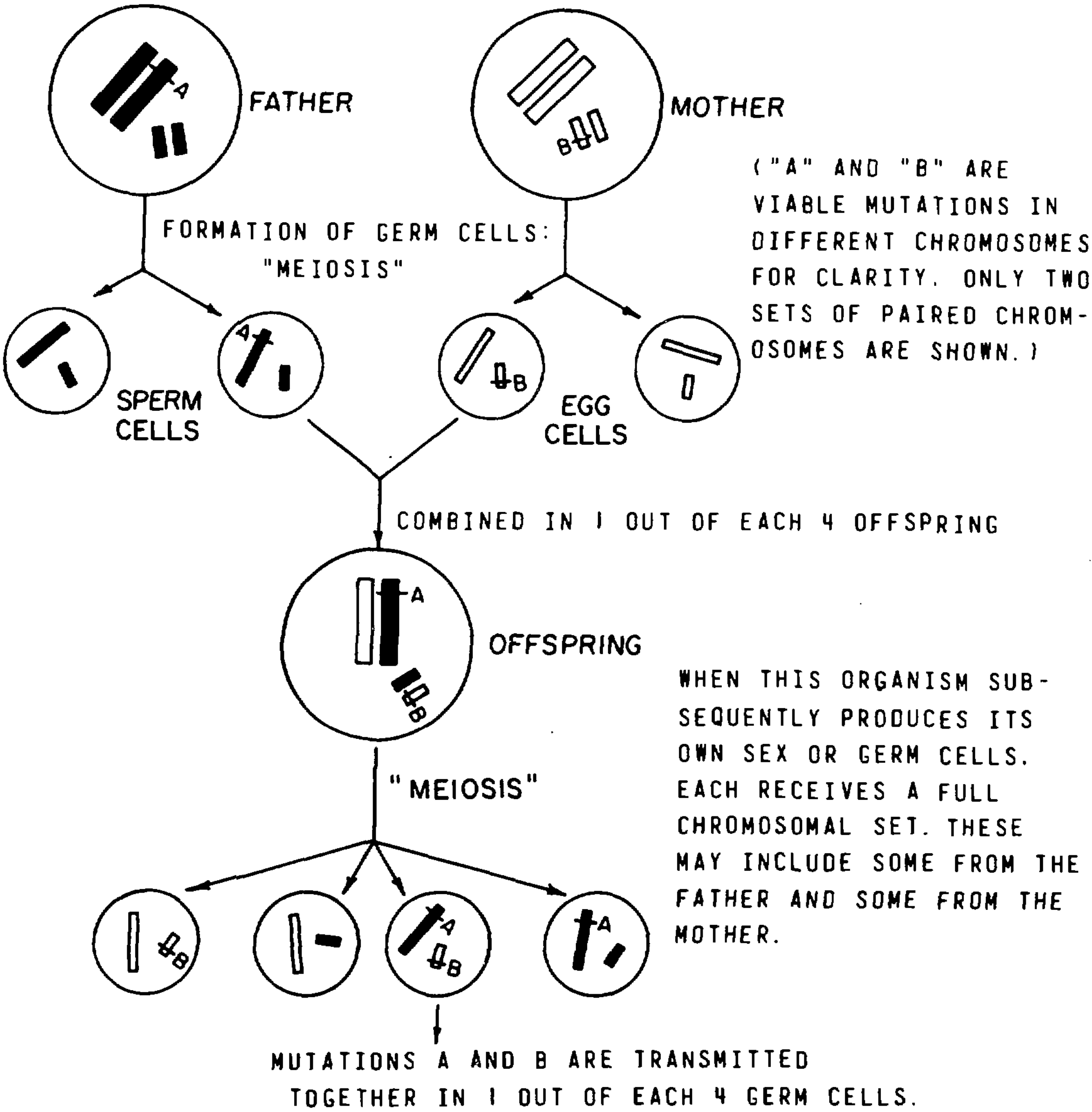


Fig.11. In sexual reproduction, the new individual or offspring is formed from the union of germ cells which are likely from different lines of descent. Variant genes which are already present in the population can be combined in different ways.

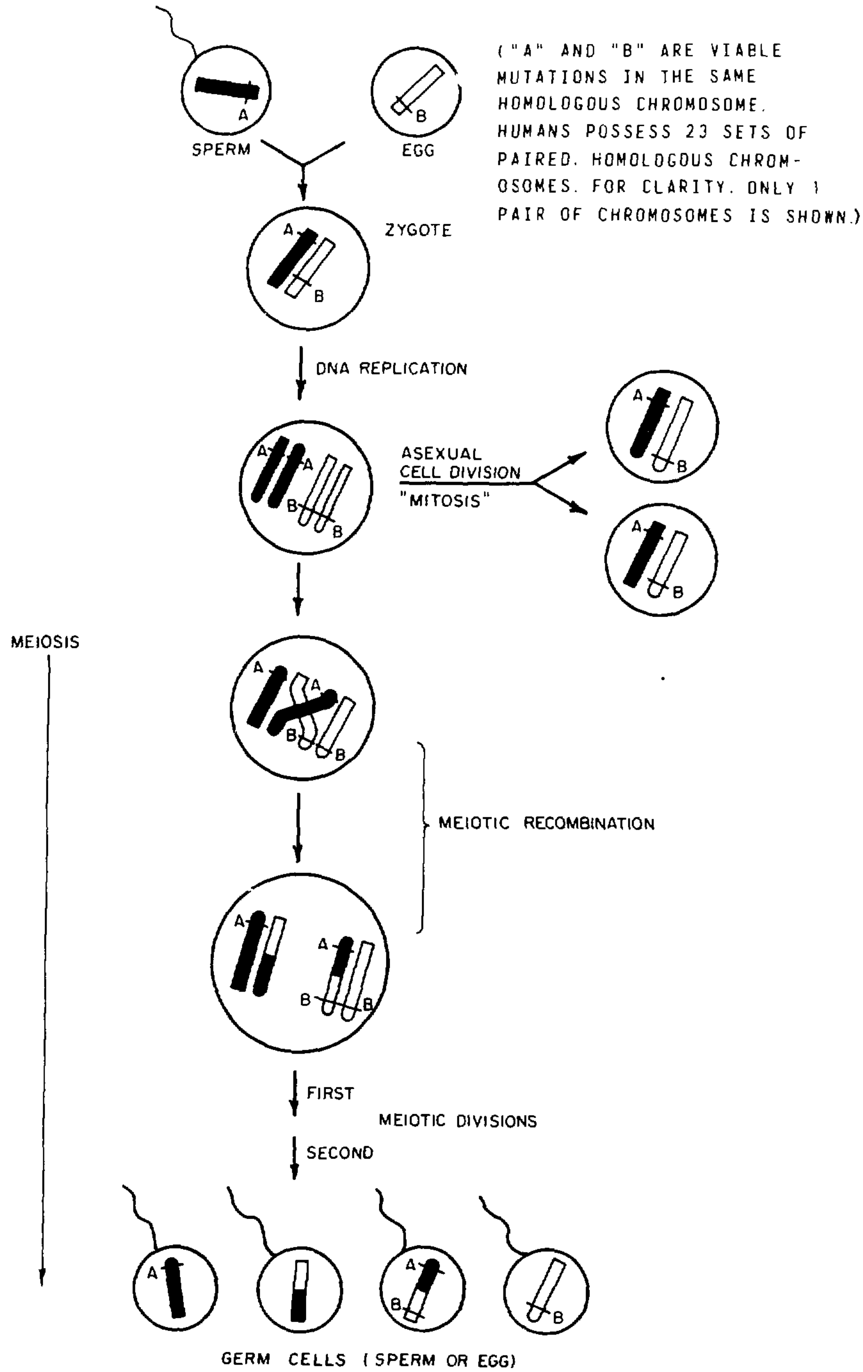


Fig.12. Recombination during formation of the germ cells (meiosis). In sexual reproduction, not only are the chromosomes randomly distributed into germ cells (Fig.11), but homologous or sister chromosomes can exchange corresponding segments (recombination) before this distribution. This generates additional combinations of variant genes. The greater the number of viable mutations or variant genes in the parents, the greater the number of possible combinations that can be generated in the germ cells.

both beneficial mutations. The chances of two advantageous mutations arising in the same cell are extremely small (the product of two very small probabilities).

Sexual reproduction, in contrast, depends on the union of two cells; these may be from different lines of descent (Fig.11). Each germ cell contains one set of chromosomes; their union produces a cell with two sets of chromosomes; one from each parent. When this organism subsequently forms germ cells in its turn, each sex cell receives one chromosomal set; some of these chromosomes may be originally from one parent and some from the other. Hence evolution in sexually reproducing species does not depend entirely on new mutations within a given line of descent; instead, genetic variants already present in the population may be brought together in the same individual. This is the major advantage of sexual reproduction; it allows the existing gene pool of the species to be tested in new combinations.

Furthermore, during the process of meiosis forming the germ cells, not only chromosomes are reshuffled but also variant genes within chromosomes. Homologous or paired chromosomes can exchange corresponding segments between themselves in the process called recombination (Fig.12). The processes involved are believed to be the same as those responsible for recombinational repair of DNA damage (Fig.8). This gene-scrambling within chromosomes and random assortment of chromosomes results in new combinations in the germ cells, but it should be emphasized that it does not represent mutation or change gene frequencies *per se*. What it does is provide new combinations of variant genes to be tested by natural selection at each generation. By producing a large amount of genetic diversity, it provides possibilities for evolution and an adaptability which cannot be achieved by an asexually reproducing species.

Some numbers on the frequency at which various genetic events occur normally may clarify this point. These numbers, which are approximations, derive from experiments that have been carried out recently at the Chalk River laboratories with yeast (Table 5). Obviously new combinations of genetic variants are generated by recombination at a vastly greater rate than that by which mutation creates new genetic variants (Table 5).

Since cells without the recombinational repair process were likely to be inactivated even by relatively small numbers of coincident damage sites, considerable survival advantage would accrue to an organism which developed the capability of performing the strand exchanges which constitute recombinational repair. This use of recombination may have been the factor in its initial selection and may have preceded its use for purposes of genetic recombination (gene assortment). According to this view the recombinational mechanism may have led to the evolution of sexual reproduction with all its advantages.

TABLE 5

Comparison of the approximate rate of generation of variability by various genetic processes in yeast

Cells in each generation with a new spontaneous mutation on a given chromosome	10^{-4} (0.01%)
Cells in which the genes on a given chromosome have been reshuffled by spontaneous recombination during normal (mitotic) cell division	10^{-3} (0.1%)
Cells in which the genes on a given chromosome have been reshuffled by spontaneous recombination during (meiotic) formation of germ cells	1 (100%)

Ionizing radiations (including heavy particles) are the most effective agents for directly producing significant amounts of double-strand breaks in DNA; these double-strand breaks would usually be lethal to dividing cells in the absence of recombinational repair. However, natural background levels of ionizing radiation would only produce one double-strand break in the DNA of a human cell once every ten years on the average (and even less frequently in the smaller amounts of DNA in a bacterial cell). A more likely source of double-strand damage would be the ultraviolet component of sunlight. Even with the current ozone layers to remove most of the ultraviolet radiation, one minute exposure to sunlight at noon on a clear June day will produce about 10,000 times more initial damage in the DNA of an unprotected cell than would be produced by exposure to natural levels of ionizing radiation for one year (see Table 3). Repair of ultraviolet damage on opposite strands by the action of the excision process (Fig.8) can also lead indirectly to double-strand breaks. To the extent that this otherwise lethal damage may have made development of recombinational repair necessary, ultraviolet radiation may be ultimately responsible for the higher forms of life.

There is another sense in which sexually reproducing species store variability, as noted earlier. In a species with biparental (sexual) reproduction, much genetic variability can remain "hidden" in each generation because the organism usually has at least two copies of the genetic material. This reduces the cost of maintaining variability. A genetic variant producing a non-functional or an altered product is not necessarily lethal to a diploid, sexually reproducing organism which carries two copies of each gene. One good copy may suffice to direct synthesis of sufficient functional protein; the fact that the other copy yields an inactive or altered protein, unable to perform the required function efficiently, is usually irrelevant. Mutations, that is, a pool of heritable variability, can thus accumulate in a sexually reproducing population without necessarily harming even the individual. Later, such mutations may become advantageous. This store of variability makes the species rich in adaptive possibilities and is a hedge against extinction of the species due to change in the environment.

GENETIC VARIABILITY - HOW MUCH EXISTS?

In practically every case where man has used artificial selection to obtain some commercially desirable trait in domesticated species, it has worked. Most of our current domestic plants and animals were produced by this method. No treatment with mutagenic agents has been necessary. This argues that populations already contain genetic variation for virtually all characteristics. Any sexually reproducing organism, like man, already has a tremendous store of variability ready for recombination. Even if mutations were to stop, the adaptive possibilities available would not decline for a very long time.

It is presently difficult to measure directly variations in DNA sequence for corresponding genes in different individuals of a species. However, variation in the genetic material can be inferred from variation in its protein products. If an unbiased sample of different specific proteins is selected, estimates can be made of the number and frequency of alleles in a population. This can be expressed as the average heterozygosity (that is, the average proportion of genetic loci at which an individual possesses two functional variants). This figure is around 13% for invertebrates and about half this for vertebrates; for man it is about 6.7%. This number refers specifically to functional variants of the genetic information, i.e. the corresponding protein product shows measurable differences in properties but can catalyse the same chemical reaction in the cell. Some of the differences between two functional proteins may be too subtle to be measured readily by available techniques in molecular biology. Moreover, various versions of non-functional DNA may be present. The above values therefore represent a minimum estimate of the degree of heterozygosity which actually exists.

However, even these figures represent an enormous store of adaptive potential. We can estimate the present possibilities for adaptive variation in man using this minimum value for heterozygosity. If there are about 100,000 gene loci in humans, an average individual would thus be heterozygous at a minimum of 6,700 loci. This person could potentially produce sex cells with 2^{6700} ($=10^{2020}$) different variations of the basic genetic information. The actual variation in genetic information in the offspring from two individuals is even greater: the other partner to a mating can produce potentially the same number of different sex cells, so the number of possible combinations is therefore 10^{4020}. This enormous number is the genetic basis for human individuality. By way of comparison, it might be noted that the total number of human beings in the world is less than 10^{10}. It is highly improbable, thus, unless two persons happen to be identical twins, that any individual carries exactly the same genetic information as any other human being that exists or has ever existed. From the genetic viewpoint, almost every human is unique. The same conclusion applies of course to the individual members of other species of plants and animals under natural conditions.

IONIZING RADIATION AND EVOLUTION

In discussing the topic of radiant energy as a natural life force, there is an inevitable tendency to concentrate on infrared, visible and near ultraviolet radiation since these particular radiations are responsible for the major portion of the radiant energy reaching the earth's surface. It seems highly probable that the origin and development of life depended on these radiations; it is certain that essentially all life on earth at present is totally dependent upon radiant energy from the sun, as indicated above (Fig.3). The role of ionizing radiation in these events seems to have been a minor one.

The levels of ionizing radiation from natural sources to which we are all exposed are normally expressed in dose units of rem and amount to about 0.1 rem per year (Fig.13). Approximately one-third of this total is derived from each of: (i) cosmic radiation; (ii) the earth itself; and (iii) the natural radioactive isotopes of constituents of our body.

Exposures to the cosmic radiation component vary appreciably; they are lowest at the equator and increase dramatically with altitude at any latitude. This increase is about 100-fold (i.e. from ~0.03 to 3 rem per year) as we go from sea-level to a height of 10 kilometres. For example, the average aircraft crew member who spends about 20 hours per week (1,000 hours per year) at an altitude of 10-12 kilometres might receive an additional radiation exposure per year of about 0.4 rem over and above that of his earthbound counterpart who spends the entire year (8760 hours) near sea-level.

Exposures to ionizing radiation from the radioactive constituents of the earth also vary considerably from one place to another (Fig.13). Although the average for most inhabited parts of the world is taken to be about 0.03-0.04 rem per year, this varies considerably depending upon the natural radioactivity of the soil and rocks.

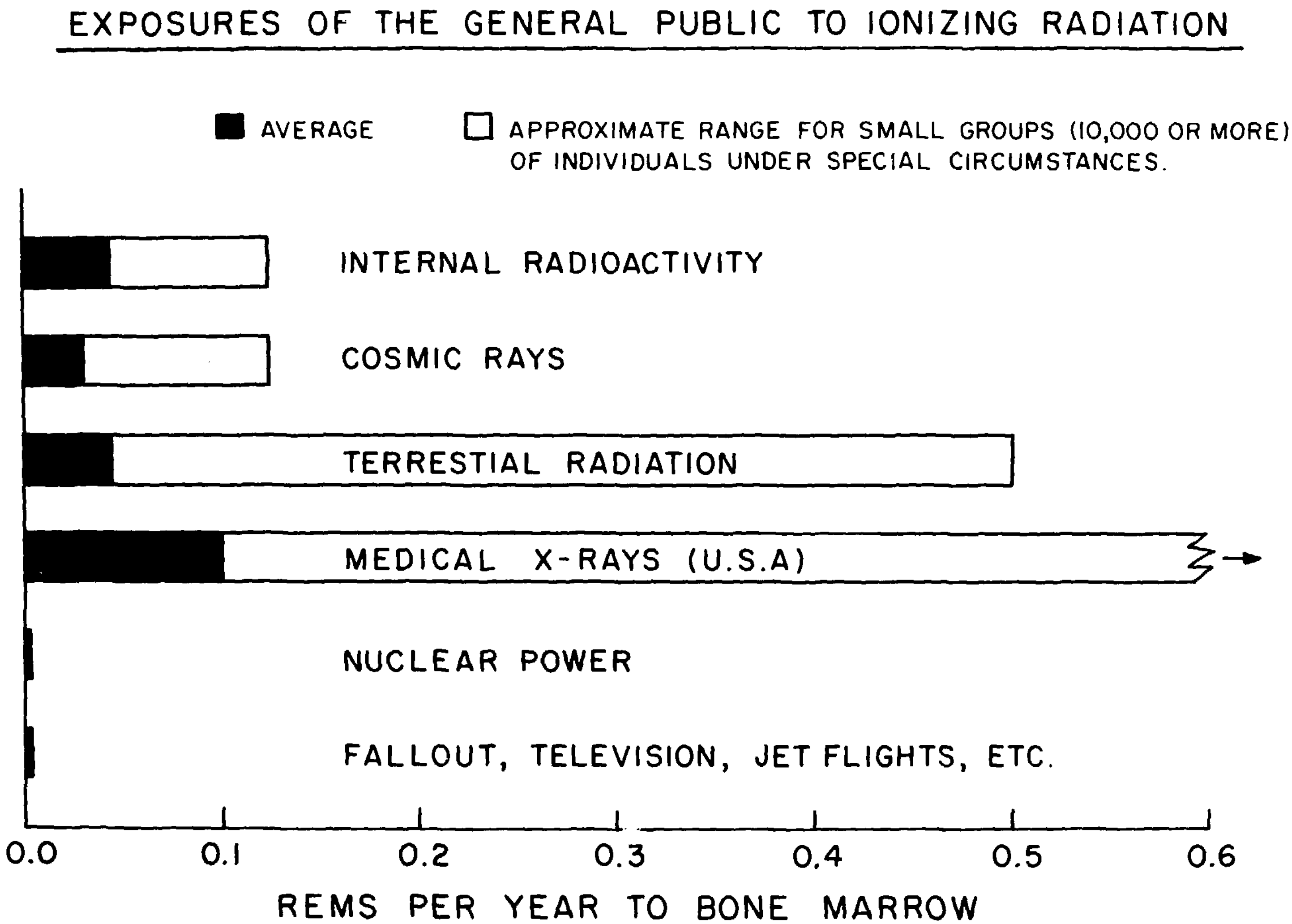


Fig.13. Variations in average exposures of the general public to ionizing radiation from various sources.

No deleterious health effects can be found in populations of humans or other animals who are exposed to levels of ionizing radiation up to about one rem per year. This does not mean that low-level radiation does not produce any harmful effects, but simply that any effects produced are much too small to be detected. Current natural exposures to ionizing radiation (0.1 rem average per year) play only a minor role in the induction of heritable changes in the genetic material which is now known as DNA (see Tables 3 and 4). Furthermore, these natural radiation levels have not changed markedly during the three billion years or so since the origin of life. Ionizing radiation from the earth is due largely to trace amounts of uranium-238 and thorium-232 which are present in all rocks, soil and sand; these radionuclides decay to 50% of their original radioactivity every 4.5 and 14 billion years respectively. The single largest contribution to the natural radioactivity of our body stems from potassium-40, a primordial radionuclide which decays to 50% of its original level every 1.3 billion years. Natural ionizing radiation levels during the origin and early evolution of life some three billion years ago would have been roughly twice their present level. Therefore, ionizing radiation has probably not played a major role at any time in the evolutionary history of most organisms.

Current exposures of the general population to ionizing radiation are much the same as they have always been (that is to say, some 30 times smaller than the levels required to double the natural incidence of mutation in humans) and are expected to have little effect, if any, on the incidence of human ill-health due to deleterious mutations. We do not yet have quantitative estimates of the numbers of new mutations caused by chemicals in the environment. However, it seems probable that most mutations are still caused, as they always have been, by natural events occurring in the DNA (for example, errors introduced during replication) over which humans have no control.

There is one indirect but important role played by ionizing radiation in the evolution of living organisms. The heat liberated during the decay of the naturally-occurring radioactive elements (uranium, thorium, potassium) in the earth's mantle is thought to have contributed appreciably to the process of continental drift. In the Paleozoic era, some five hundred million years ago, the precursors of all the present continents were evidently combined into one large super-continent currently called Pangaea. According to the theory of plate tectonics, the present configurations of the continents are a consequence of the latest episode of continental drift, beginning 200 million years ago.

A diversity of life forms has evolved on these land areas since that time, owing to the physical isolation of the land masses. Some of the most remarkable examples of this diversity occur on the continent of Australia which did not have any placental mammals before humans migrated to this continent. However, the continent provided a home for a wide variety of herbivorous and carnivorous marsupials, each of which occupied the same sort of niches in the general ecology that were occupied by placental mammals on other continents. Other less dramatic examples of diversity have evolved on each of the land masses that have become separated due to continental drift, and even between species on a given continent which have become separated by the mountain ranges formed in the same processes. To the extent that heat from natural radioactivity in the earth has contributed to the present form of our continents, it has thus also contributed to the diversity of living organisms.

PROGNOSIS FOR THE FUTURE?

Our own species is a product of evolution. Natural selection must have been responsible for this evolution. Mankind is still evolving; indeed, it is very young for a species. We do not know where it is heading (this will be determined by future circumstances) and can only speculate to what extent man may direct, affect or terminate his own evolution. Man, more than any other species, might develop the potential to control his own evolution. We do know that recent progress has depended more on what humans did with their environment and technology than on what they did with their genes. Man has tended to change his environment to suit his genes, rather than the converse. Whereas birds became fliers by hundreds of millions of years of evolution, man has become the most powerful flier of all, but by constructing flying machines, not by reconstructing his genotype. Presumably the same principle will continue to hold in the immediate future as humans expore the possible uses of their natural environment, although recent research on recombinant DNA does provide some indications that humans will be able in the future to manipulate the genes of selected organisms to their own benefit.

There is little doubt that humans have already altered evolutionary processes for their own benefit. Other species of animals which are considered harmful to humans have in general been reduced to small numbers, and humans have acted as conscious agents of evolution in the selective breeding of domestic animals and plants. Selective pressures (for example, famine, disease) against deleterious genes in humans have also been reduced in many areas of the world. Some geneticists have warned of the potential for harm resulting from what might be interpreted as a gradual erosion of our genetic constitution. Modern medicine, sanitation, and social practices have certainly saved the lives of many individuals who might otherwise have died before reproductive age because of genetic disabilities. There is not at present much evidence to indicate that this is a serious problem. First, the more serious genetic defects in human populations rarely reproduce, even with the advantages of modern medicine. Second, approximately 90% of the human ill-health which has a genetic component is thought to be maintained by past selection pressures in favour of the variant genes; heterozygote superiority and hybrid vigour are two general examples of this. A continued change in the conditions under which people live will undoubtedly lead to slow changes in the genetic characteristics of human beings over very long periods of time. It does not, however, seem profitable to attempt to predict the probable direction of these future evolutionary changes.

The concepts outlined here are all a direct result of basic research in various areas of science. An attempt has been made in this review to integrate concepts from the fields of chemistry, physics and biology, each of which represents an artificial, if necessary, division of human knowledge of the universe. Basic research in the specialized area of radiation biology has made an appreciable contribution to our understanding of biological evolution and the role of radiation as a natural life force. At one time, both the mechanisms of life and the origin of the vast diversity of living organisms on the earth appeared to be shrouded in mystery. Our history books record many speculations on the origin of life and of human beings. A large number of distinct advances in knowledge over the past 150 years has been involved in the elucidation of current understanding of the actual events involved. There is no reason to believe that the concepts outlined here will not require amplification and appreciable revision in details within a decade or two as a result of further research into the nature of the universe in which we live. The main outline, however, does seem fairly clear and has not altered drastically since the time of Darwin. Given current understanding of molecular biology, it appears relatively simple now to describe the mechanisms by which a simple bacterium can evolve into a more complex organism such as a mammal.

One other point may be of interest in conclusion. There is no direct proof available to us as yet that living organisms of some kind actually exist elsewhere in this galaxy or in the universe. From our present understanding of the evolution of life on earth, and the role of radiant energy as a natural life force, this conclusion does, however, seem highly probable. The processes of the creation and evolution of living organisms (including ourselves) appear to be explicable as the inevitable natural consequence of chemical and physical laws. There is thus no reason to suppose that similar events have not occurred elsewhere in our galaxy and in other galaxies or that radiation energy has not played the same vital role in these events elsewhere in the universe as it has done on this planet earth.

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This paper is dedicated to our favourite heterozygotes.

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