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Review article

A planet in motion: past and present of biological clocks

Un planeta en movimiento: pasado y presente de los relojes biológicos

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Abstract

Biological rhythms are a fundamental part of the life of organisms and are closely related to geological movements and periodic environmental changes, such as temperature, humidity, and light. These biological rhythms have developed over time as an evolutionary response to environmental pressures, leading to the formation of genetic circuits that control biological time and regulate the physiology and behavior of living beings. The perception of light is a key factor in the development of biological rhythms since it provides an external signal to adjust the internal biological clocks of organisms. Photolyases and photo perception mechanisms developed in living beings throughout evolution have allowed adaptation to these signals and the formation of the circadian system, which is responsible for regulating daily and annual biological rhythms. In all living beings, there is a circadian system; in mammals, it is in the suprachiasmatic nucleus. The genetic circuit of the internal clock of organisms must be well established at all levels of the organism, since it is essential to regulate the fundamental behaviors of these, such as feeding, reproduction, or migratory processes. The biological rhythms also play an important role in adapting organisms to different geographical areas and seasonal changes. This review addresses the evolution of biological rhythms, whose functionality plays an important role in the adaptability and success of species in response to the changing external patterns of our planet.

Keywords: Earth evolution; photobiological processes; environmental adaptation; biological rhythms; circadian system; UV rays.

Resumen

Los ritmos biológicos son una parte fundamental de la vida de los organismos y están estrechamente relacionados con movimientos geológicos y cambios ambientales periódicos, como temperatura, humedad y luz. Estos ritmos biológicos se han desarrollado a lo largo del tiempo como una respuesta evolutiva a las presiones ambientales, lo que ha llevado a la formación de circuitos genéticos que controlan el tiempo biológico y regulan la fisiología y el comportamiento de los seres vivos. La percepción de la luz es un factor clave en el desarrollo de los ritmos biológicos, ya que proporciona una señal externa para ajustar los relojes biológicos internos de los organismos. Las fotoliasas y los mecanismos de fotopercepción desarrollados en los seres vivos a lo largo de la evolución han permitido la adaptación a estas señales y la formación del sistema circadiano, responsable de regular los ritmos biológicos diarios y anuales. En todos los seres vivos existe un sistema circadiano; en los mamíferos, este se encuentra en el núcleo supraquiasmático. El circuito genético del reloj interno de los organismos está bien establecido en todos los niveles del organismo, y es esencial para regular comportamientos fundamentales como la alimentación, la reproducción o los procesos migratorios. Los ritmos biológicos también desempeñan un papel importante en la adaptación de organismos a diferentes zonas geográficas y cambios estacionales. Esta revisión aborda la evolución de los ritmos biológicos, cuya funcionalidad juega un papel clave en la adaptabilidad y el éxito de las especies en respuesta a los patrones externos cambiantes de nuestro planeta.

Palabras clave: Evolución de la Tierra; procesos fotobiológicos; adaptación ambiental; ritmos biológicos; sistema circadiano; rayos UV.

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1. Introduction

The adjustment of biological rhythms to environmental periodicity is essential for the survival and reproductive success of species. The ability of organisms to synchronize with the daily and seasonal cycles of our planet allows them to anticipate these variations, preparing them for situations such as food availability, migration, reproductive mating, and hibernation. However, when there is a mismatch between biological rhythms and environmental signals, functional and behavioral problems occur that can lead to a decrease in the physical and reproductive fitness of individuals.[1,2] Environmental cues are grouped into proximate and past cues (factors), and together they determine the timing of a physiological event. Proximate cues include day length, temperature, humidity, and food availability. In contrast, late cues are associated with the culmination of a physiological event at the most appropriate time during a defined temporality.[2] In particular, the photoperiod -the duration of daylight- is a crucial environmental cue that influences the timing of many biological processes, such as plant flowering and animal reproduction, among others.[2,3] Light has also played a fundamental role in the evolution of species over millions of years. Organisms have adapted to changes in the light spectrum associated with Earth's seasonal and geological cycles. Consequently, the ability of organisms to perceive and respond to light is a common feature along the phylogenetic scale. The speciation of organisms has led to the evolution of light perception and response mechanisms, but also of protection, such as the expression of photolyases and the circadian system, allowing organisms to adapt to changing environmental signals.[4,5]

2. The Earth and its cycles at the beginning of life

To understand the origin of life on our planet and the conformation of its cycles, it is essential to consider the geological ages that have shaped its evolution.[5,6] These ages are divided into two major time intervals: the Precambrian Eon and the Phanerozoic Eon. The first eon, which occupies about 90% of Earth's geological history, began with the planet's formation around 4.5 billion years ago and extended until approximately 570 million years ago. This period, known as the Precambrian, is subdivided into three eras: the Azoic, Archeozoic, and Proterozoic. During the Azoic era, no recognizable life existed. It is believed that during this period, the formation of the oceans and the primitive atmosphere of the Earth, rich in gases such as hydrogen, methane, and ammonia, occurred. The Archeozoic and Proterozoic eras, which extend from about 4,000 million years ago to about 2,500 million years ago, are where important geological and biological changes took place.[7] During these eras, the Earth underwent the formation of continents. It is believed that the first RNA molecules were formed in the aqueous medium, and there was the appearance of the first unicellular organisms, such as bacteria and archaea. These living beings developed in aquatic environments and, in some cases, were capable of photosynthesis. To give way to all these changes, it is important to understand the composition of the universe since the Earth was formed with these elements that gave way to more complex compounds. It is known that the general composition of the universe is mainly 90% hydrogen and 9% helium, these being the most abundant elements in the cosmos; however, the remaining 1% is made up of a variety of elements, including oxygen, nitrogen, neon, argon, carbon, sulfur, silicon, and iron.[8] This knowledge

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has allowed us to infer that the Earth, in its beginnings, had an atmosphere composed mainly of water vapor, ammonia, methane, hydrogen sulfide, hydrogen cyanide, and other hydrogen compounds, which mixed in the primordial ocean.[9] The hypothesis is that for life to start, both elements and elementary molecules needed to combine to form more complex molecules, which required a constant supply of energy.[10] This energy contribution was provided by sunlight, especially in its ultraviolet (UV) radiation content, which, when incident on the ocean, supplied the necessary energy for small molecules to form larger ones.[11] Thus, sunlight played a fundamental role in the origin and development of life on Earth. The interaction of the dynamic physical and chemical processes that took place in this evolutionary moment of the planet, gave way to the formation of different systems that were distributed in: Earth's crust, hydrosphere, and atmosphere, and two external subsystems that influenced decisively on Earth: the Sun, and the Moon (the latter, practically with the same age as our planet).[7-12]. The Moon has exerted a significant gravitational influence on the Earth since it has a stabilizing effect on its axis of rotation. The obliquity of the Earth's axis (which is around 23.5 degrees) is responsible for seasonal changes and the distribution of sunlight at different latitudes. It is precisely this lunar dynamic that contributed to the stability of the planet, especially regarding how the Sun's rays arrive and the amount of UV rays.[7-12] It is well known that the length of the day and the night are determined by the Earth's rotation on its axis, which has been fairly stable throughout geological time, however it should be noted that although the length of the day has varied slightly due to the gravitational influence of the Moon currently, the cycles of 12 hours of light and 12 hours of darkness in the tropics are not a direct consequence of lunar dynamics, but rather of the angle of inclination of the Earth's axis and its orbital movement around the Sun.[12,13]

Regarding the influence of the Sun, it is known that about 3.5 billion years ago, at a time when solar activity was 30% less than today, high concentrations of carbon dioxide (3% compared to the 0.04% current) generated a significant greenhouse effect that kept the temperature of the oceans stable.[14] During that time, the Earth was covered by an abundant amount of volcanic ash, which resulted in a considerably thin atmospheric layer. Consequently, there was a decrease in the initial greenhouse effect. This phenomenon was caused by intense volcanic activity since the formation of the ozone layer took place millions of years later.[14] Due to these fluctuating changes, UV rays could easily penetrate the atmosphere. All these characteristics were essential to give rise to the first organisms that found an environment conducive to the evolution of other beings that used molecular oxygen (O_2), a vital element for aerobic organisms, including all animals.[14] It is believed that the photosynthetic processes of ancestral cyanobacteria (unicellular prokaryotes without a defined nucleus) were responsible for the presence and increase of O_2 in the hydrosphere and atmosphere.[14] With the accumulation of O_2, the atmosphere increased its thickness and reached a greater height, which caused the dissociation of the O_2 molecule by UV radiation, which would later recombine to form triatomic oxygen molecules, ozone (O_3). This ozone layer works as a highly effective filter, preventing the passage of UV radiation that damages the genetic material of organisms. This fact constituted one of the key factors that determined organic evolution on Earth.[15] In turn, UV rays may have triggered the emerging genetic mechanism of storing information in more than one gene, as a way of limiting mutations.[16] This has been corroborated by the discovery of fossil structures called stromatolites, formed by the capture and fixation of mineral particles and organic

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matter by photosynthetic bacteria, which accumulate over time in a stratified manner.[17,18] As noted in various studies, "these 3.5-billion-year-old microbial ecosystems played an important role in creating an oxygen-rich Earth atmosphere and in the evolution of life from simple forms of single-celled organisms to complex multicellular forms that we see today" (Figure 1).[19]

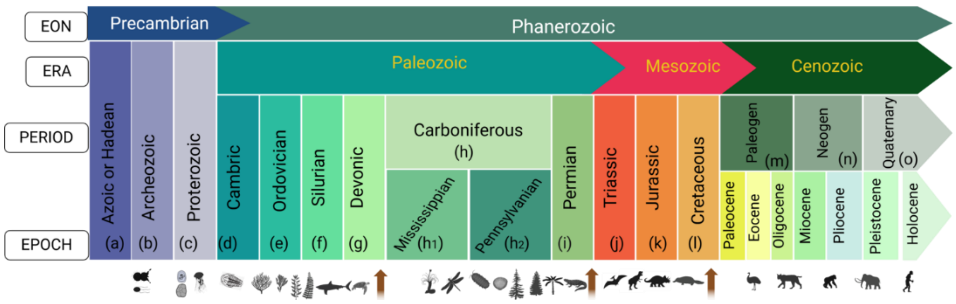

Figure 1. Precambrian Eon (4600- 542 Ma), which covers three Periods: Azoic or Haldean, Archeozoic, and Proteozoic (a, b, c). It begins with the formation of the Earth and its Moon. Life and its diversification begin. Emergence of prokaryotic cells (bacteria and cyanobacteria) and eukaryotes. The first photosynthetic cells, perhaps like current cyanobacteria, were found in the oldest known fossils called stromatolites. The formation of continents, oceans, the oxidizing atmosphere, and the ozone layer begins. Phanerozoic Eon (542 Ma to present), which covers three Eras: Paleozoic Era (Periods: d, e, f, g, h, i). Many geological and biological processes occur, modifying the shape and structure of the Earth, as well as the diversity of life over millions of years. At first, life was mainly confined to the seas. Subsequently, the diversification of invertebrates and organisms with exoskeletons occurred. The first terrestrial animals and vascular plants appeared, developing large forests of ferns and lycopods. Consequently, there were high concentrations of oxygen in the atmosphere, leading to the appearance of large terrestrial organisms. At the end of this Era, the largest mass extinction in Earth's history occurred. Mesozoic Era (Periods: j, k, l): Appearance and heyday of the great dinosaurs, called the "Age of Reptiles". The first flying organisms appear, and later true birds. In this stage, mammals and gymnosperm plants, among others, emerged, which determined the course of current life on Earth. Two mass extinctions occurred, the first at the end of the Triassic period and the second at the end of the Cretaceous (75% of species). Cenozoic Era (Periods: m, n, o): The most important changes that occurred gave rise to the flora and fauna that currently exist, among these are the evolution of mammals (also known as the "Age of Mammals") and the appearance of the human being. During this Era, events occurred such as: the continents were acquiring their current positions, the Atlantic and Indian oceans opened, and the two parts of the American Continent were also joined by the Isthmus of Panama due to the collision of the Euro-Asian Plate and African. The climate was characterized by gradual cooling and some ice ages. Taken and modified from Arrows indicate major species extinctions. Taken and modified from: https://portalacademico.cch.unam.mx/interactivos/eras-geologicas/.

3. Solar radiation and life

The influence of solar radiation extends to both terrestrial and aquatic ecosystems. It directly controls photobiological processes such as photosynthesis, photoperiod, and phototropism. Additionally, solar radiation affects other environmental factors like temperature, humidity, and the daily, annual, and water cycles. These factors, individually or collectively, influence the distribution of organisms.[20]

The solar radiation that reaches the Earth covers a wide range of wavelengths in the electromagnetic spectrum. Approximately 40% of this radiation corresponds to visible light, which extends in wavelengths from 400 to 700 nm. Such a range includes violet, blue,

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green, yellow, orange, and red light. This radiation is essential for plant photosynthesis and is known as photosynthetic active radiation (PAR). In addition to the PAR range, solar radiation includes a range that extends from 280 nm to 1000 nm and is known as the photobiological range since it is involved in additional processes controlled by specific photoreceptors such as phytochromes.[21] Lastly, high-intensity solar radiation, that is, when the proportion of short waves exceeds certain limits, can be detrimental; therefore, the amount and intensity of radiation due to changes in the spectral composition can affect important processes in the organisms. Among the wavelengths that make up solar radiation is UV light, considered one of the most influential in the evolution of living beings.[22] UV radiation is divided into three components: UV-A, which extends from 400 to 315 nm, is little absorbed by O_3, and reaches the Earth's surface in greater quantity. UV-A constitutes an important photomorphogenic signal in plants and animals and is the least harmful.[23] UV-B radiation, which covers wavelengths between 315 and 280 nm. This radiation comprises a small region of the electromagnetic spectrum; however, its action on plants and animals is considerable since important biomolecules such as proteins and nucleic acids absorb it strongly.[24] Although there are positive effects attributable to this radiation, such as growth and development in plants, in large quantities, it can have harmful effects, especially at the genetic level.[23,24] Finally, UV-C radiation, which extends between 280 and 100 nm, is the most energetic and considered the most damaging to DNA. However, because it is the most absorbed by O_2 and O_3 in the stratosphere, it practically does not reach the Earth's surface when these gases are present.[24,25]

Throughout the evolution of life that began in the oceans, living beings developed strategies to avoid the effects of damaging UV radiation.[22-26] These strategies are reflected in the vertical migrations of zooplankton either in the oceans or freshwater bodies. This event by itself has been so important that it is considered to it could be the evolutionary origin of photoreceptors and circadian rhythms.[26] In these aquatic organisms, the first major strategy involves enzymatic systems to repair DNA damage induced by UV radiation.[22-26] The second strategy involved protective pigmentation (e.g., carotenoids). The third strategy has been to avoid UV radiation, where organisms descend into the deeper water body during the day. These so-called "vertical migrations" of planktonic animals were detected during World War II when seabed sampling was carried out with sonars.[27,28] In these samplings, a phenomenon called "the deep dispersal layer" was revealed. This layer consists of organisms, mainly crustaceans (copepods) and mollusks, and moves near the water surface at night and descends in the morning until it reaches its greatest depth at noon, rising again at night.[29] The most accepted hypothesis to explain these movements is that light initiates and controls vertical migrations, since organisms respond negatively to light, especially UV radiation.[30,31] Subsequently, precision echo sounder studies showed that the zooplankton sound-scattering layer tends to align with a blue-light isolume on the order of 5×10^{-4} μW cm^{-2} at ~474 nm, with reported thresholds varying by site and taxa (≈ 0.005–1 μW cm^{-2} in other systems). From these data, it is now known that the daily vertical migrations (diel: 24-hour period, relative to animal behavior) of these organisms are primarily linked to light conditions.[32,33] In studies carried out in seas at polar latitudes, it has been observed that the vertical distribution of zooplankton is constant, since it occurs during the continuous diurnal period of the Arctic summer, while in autumn, when the alternation of day and night is evident,

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the movement of vertical migrations resumes.[34,35] In this sense, it is considered that the vertical migration of plankton aggregates occurs in an optimal band of light intensity, moving phototactically towards the light source or away from it. The ability and speed of planktonic organisms to move photokinetically depend on the light intensity since it has been shown that they can migrate at minimum speeds even in complete darkness through phototaxis, photokinesis, or a combination of both.[36] Phytoplankton also present daily activity influenced by light, as is the case with blue-green algae. The pattern of daily activity of these organisms is observed in their photosynthetic activity, since it presents an increase in the rate of photosynthesis in the early hours of the morning, reaching a maximum when the light intensity reaches the saturation level, subsequently decreasing at noon when light intensity reaches inhibition levels.[37] Another maximum peak occurs during the afternoon when the light intensity decreases, and finally begins a gradual decrease in the photosynthetic rate while the light intensity is progressively reduced.[37]

In general, UV radiation intervenes as an important selective force for zooplankton and phytoplankton, demonstrating that these species migrate to a depth of optimal light intensity to avoid damage by UV radiation.[38] In precisely this sense, Pittendrigh and his colleagues proposed that "light escape" was an important evolutionary driving force for the development of circadian rhythms.[39]

However, although UV radiation has been shown to affect zooplankton and phytoplankton behavior, other factors can also influence vertical migrations, such as food availability, temperature, and the presence of predators.[40] Furthermore, while the coevolution of photoreception and circadian rhythms is an important research topic, its relationship to diel vertical migrations is not fully understood, and the subject remains under study.[41]

4. Photolyases and DNA repair

Geological studies have provided evidence that, in the Precambrian, the atmosphere was low in O_2 due to the lack of the protective layer of O_3. As a result, primitive organisms were exposed to high doses of UV radiation during the day, causing serious DNA mutagenesis (around 260 nm, where DNA absorbs it) due to the formation of photoproducts.[42] Thymine (T's) dimers formed by two consecutive T's on the same strand, and the photoproduct formed by pyrimidine-pyrimidine dimers between adjacent bases on the same DNA strand are the most important. To protect organisms from these photoproducts, a coevolution of enzymes called photolyases, which are flavoproteins involved in the repair of DNA damaged by UV light, evolved.[42] Photolyases are phylogenetically ancient enzymes present from prokaryotic organisms to eukaryotes. The activation mechanism of photolyases occurs by blue light (474-600 nm), and they contain flavin-adenine dinucleotides (FAD) as a catalytic chromophore and a second chromophore involved in light harvesting. The second chromophore is methenyltetrahydrofolate (MTHF) or a deazaflavin (7,8-dimethyl-8-hydroxy-5-deazariboflavin,8-HDF).[42] Excitation energy from the light-harvesting chromophore is transferred to the catalytic chromophore, and photolyases selectively bind pyrimidine dimers in UV-damaged DNA and move an electron from the excited state of the flavone to the pyrimidine dimer, which then repairs the DNA damage by isomerization to produce the original two pyrimidines. There are two types of photolyases (type I and type II) that repair cyclobutane pyrimidine dimers, and another class involved in the repair of photoproducts (6-4), first identified in the fruit fly (*Drosophila melanogaster*).[43] The fact that photolyases are activated by blue light is not a coincidence, since

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only blue light reaches great depths in the aquatic environment, where the first organisms evolved and continue to evolve today.

5. Cryptochromes and the circadian clock

Cryptochromes (CRY) belong to the same family of proteins as light-activated photolyases. These proteins are blue light photoreceptors and are present in both plants and animals.[42-44] In many species, cryptochromes are involved in resetting the circadian clock as phylogenetic analysis of the cryptochrome-photolyase (CFP) family suggests that cryptochrome blue light photoreceptors have evolved from photolyases having an enzymatic activity that has evolved into an internal clock signaling mechanism.[44]

Cryptochromes were first identified as blue light receptors in plants (i.e., *Arabidopsis thaliana*). In these, it was observed that their proteins show a strong similarity with photolyases.[44] They also use FAD and MTHF as chromophores but lack detectable photolyase activity. *Arabidopsis* CRY1 and CRY2 proteins function as blue light receptors on circadian rhythm input.[45] The first indication that cryptochrome receptors also existed in both animals and humans was through the finding of a *Drosophila* photolyase-related gene, the 6-4 gene.[46,47] In these works, a mutant gene (*cryb*) was isolated from a transgenic line of flies carrying a luciferase reporter gene fused to the period clock gene (*per*). In wild-type flies, the expression of the luciferase reporter oscillates with their circadian rhythm, while the *cryb* mutation lacks cyclical expression of it, as well as other clock RNAs. As the RNA cycle is reset by temperature input, it was suggested that light input was affected by the mutation.[48] Although recent data suggest that CRY might also be a part of the central oscillator in *Drosophila*, the evidence strongly points to CRY as a circadian photoreceptor most involved in light entry in this organism.[46,47] Given the similarity between photolyases and cryptochromes, it is suggested that both circadian photoreceptors originally functioned in the photorepair of damaged DNA. Subsequently, they intervened in the avoidance reaction to UV radiation, especially detecting the decrease in luminosity that signals the arrival of night and the time to return to the surface in aquatic organisms.[48] This phenomenon occurs because only blue light penetrates deep into the scattering layer.[49]

A new component of the circadian clock, *casein kinase 2α*, was identified in D*rosophila*. This is a selective serine/threonine kinase consisting of a tetramer of two alpha subunits and two beta subunits. *Alpha* subunits possess the catalytic domain with kinase activity.[49] Its importance resides in the fact that this enzyme is involved in the circadian clock mechanism, responding to UV damage in organisms, from yeast to humans, which supports the important role of light in the origins and evolution of biological rhythms.[50] Because photolyases interact with DNA, it is reasonable to think that the behavioral response of aquatic organisms to the 24-hour light-dark cycle also involves direct cryptochrome-mediated changes in gene expression.[48-50] This suggests that organisms then developed a more sophisticated temporal program, in which they acquired the ability to anticipate the light-dark cycle, which implied behavioral changes even in the absence of changes in light intensity, that is, a free-running circadian clock. Through these findings, it is suggested that sunlight induces an optimal fit for an early evolutionary relationship between blue light photoreception and circadian rhythmicity.[51] This evolutionary relationship for the photoperception of the different wavelengths of sunlight (particularly blue light) is evident in organisms with vision.[51,52] Visual information is transferred directly to effector organs, e.g., flagella, and muscles, or processed in the brain to generate a perception of the three-dimensional world, and provides animals with time-of-

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day information. Light-time signals couple endogenous circadian rhythms that are close to 24 hours to the precise 24-hour cycle of the Earth's rotation. Therefore, the circadian system provides a representation of the fourth external dimension, time.

6. Photoreceptors and the circadian cycles

Photoreceptors are specialized cells found in both animals and plants that contain light-sensitive pigments and convert light energy into electrical signals that can be interpreted by the body.[52] As multicellular organisms arose and specialized cells developed for specific tasks, therefore not only did cell diversity related to light absorption increase, but these cells began to organize themselves into increasingly complex organs, adding new functionalities with each evolutionary step. In the case of plants, this process has been less noticeable, since the organs in charge of detecting light, although more complex, have followed a functionality like that of protist microalgae.[53,54] The first form of multicellular association that could have given rise to a light-sensing organ in animals is called an *ocellus*. It consists of a flat layer composed of a few cells specialized in light absorption, superimposed on a layer of pigment cells that act as a screen.[51,52] Although these organs may seem very simple compared to the human eye, for example, at the time, they represented a clear evolutionary advantage. The ability to differentiate between light and dark allowed species with *ocelli* to perform phototactic movements, unlike those without them. In these organisms, cellular specialization is not observed, and all the structures related to light capture are called organelles, formed by groups of cells that generate structures with specific functions.[51,52] These photosensitive pigmented organelles (like *opsins*) absorb light and carry out processes of phototransduction that generate electrical information. These currents report the presence or absence of light in the environment, generating a direct action on motor cells that triggers movement patterns in response to light, called phototaxis.[54,55] As organisms evolved towards multicellular forms, this structure became more sophisticated, incorporating cells specialized in capturing light, thus allowing adaptation to periodic changes in light and, consequently, regulating their biological cycles. Today, animals that have moved up the evolutionary ladder detect light waves through photoreceptors known as rods and cones, located in the eye retina.[56,57] These photoreceptors transmit electrical signals to the brain via the optic nerve, where they are processed and interpreted as visual images. In plants, the most important photoreceptors are the so-called phytochromes, cryptochromes, and phototropins, which allow them to detect the intensity, direction, and quality of light.[53-58] In the visual system of various organisms, including humans, the response to light is produced by visual pigments called opsins present in the lipid bilayer of the rods and cones of the retina.[58] The rods, which contain rhodopsin, are responsible for vision in low-light conditions and are most sensitive to a wavelength of 500 nm, corresponding to blue-green light. On the other hand, cones contain three different types of opsins: one that is more sensitive to long wavelengths (red light), another that is more sensitive to medium wavelengths (green light), and another that is more sensitive to short wavelengths (blue light).[59] These opsins belong to the family of G protein-coupled receptors, and their ligands are chromophores derived from vitamin A, usually integrated into the cell membrane. Chromophores produce color because they can absorb specific wavelengths of visible light and transmit or reflect them. The retinal rods that act as circadian photo-

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receptors in mammals connect to the suprachiasmatic nucleus (SCN) and are made of rhodopsin.

In addition to cones and rods, there is a special group of ganglion cells called "intrinsically photosensitive retinal ganglion cells" (ipRGCs), which constitute a third class of photoreceptor within the retina, characterized by the expression of the photopigment melanopsin. These cells represent between 0.3% and 0.8% of the total retinal ganglion cells, and their roles are diverse and crucial, including from the image-forming vision to the regulation of circadian rhythms or the activation of the light pupillary reflex (PLR).[59] In the regulation of circadian rhythms, the activation of ipRGCs induced by light sends information through retinohypothalamic projections to the main circadian pacemaker, located in the hypothalamic region of the CNS. On a smaller scale, ipRGCs project to the olivary pretectal nucleus, regulating the PPR. In this regard, a close relationship between the robustness of the circadian system and ipRGCs has been demonstrated; however, not all cells containing melanopsin project outside the retina, and some studies have shown the existence of melanopsin interneurons in the mammalian retina.[59] The functional integrity of the circadian system partially depends on the integrity of melanopsin-secreting cells as an essential component.

In *Drosophila melanogaster*, rhodopsin also contributes to circadian photoreception; however, it was shown that important cryptochromes that function as chromophores are involved in this phenomenon: FAD and MTHF.[60] Mammalian cryptochromes also act as circadian photoreceptors, as they are important components of the central clock. Cryptochromes are closely related to photolyases, which led to the idea that the DNA-binding property of photolyases was conserved in cryptochromes.[61,62] In this perspective, many authors have suggested that the strong UV component of sunlight contributed to the selective pressure for the evolution of this specialized photoreceptor, which led early metazoans to avoid irradiation by descent into the oceans during the day. Therefore, it is no coincidence that blue light photoreception evolved in an aquatic environment since only this type of light can penetrate to substantial depths in water.[61] This provided an optimal fit for the presence of blue light-dependent photoreceptors and a very early relationship with circadian rhythmicity.[61,62]

7. The hands of the molecular clock: the genes

Circadian rhythms are generated by a group of genes known as molecular clock genes, whose protein products are necessary for the regulation of biological rhythms. These genes are involved in a *transcription/translation gene and protein clock feedback loop* (TTFL), which is self-sustaining in cycles of approximately 24 hours.[63]

The components of the molecular clock systems have been characterized in a very specific way in vertebrates, insects, plants, and fungi.[64] From these studies, it is known that the interaction of clock genes and their feedback loops is conserved across *phyla* and is extraordinarily robust, but there are also many variations, so the divergence of the molecular and functional components could be explained in part by the duplication and/or loss of genes throughout evolution. This same evolutionary process has allowed circadian synchronization to be common to practically all living beings and allows anticipate the regular environmental changes that influence them. These include food intake and metabolism, predator/prey interactions, and DNA damage evasion from environmental insults, among others.[65] Circadian rhythms allow an organism at the molecular level to achieve temporary homeostasis with respect to its environment, being the result

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of a regulation of gene expression and generating a peak of protein expression once every ~24 h.[65,66] This defines and controls the time when a particular physiological process is most active with respect to the solar day. For example, DNA damage from solar radiation is preferentially repaired (via the nucleotide excision repair pathway) at the end of the day or early night, whereas the ability to repair such damage is low before dawn.[67] The temporal regulation of this event has a critical role in maintaining genomic integrity and is conferred by the circadian clock through the control of protein expression, being rate-limiting factors in UV excision repair.[67] The importance of integrity in the oscillation of clock gene expression in a circadian period results in the interaction of the above-mentioned components in interrelated feedback loops, and whether such genetic mechanisms control circadian activity in the species.[66] Specifically, from the studies carried out in *Drosophila*, it was possible to identify genes that are involved in processes of regulation, creation, and maintenance of many biological rhythms (for example: the sleep-wake cycle, food intake, or hormonal expression, among others).[68] In mammals (mice, hamsters, rats, rabbits, guinea pigs), homologous genes were subsequently identified where at least nine clock genes had been described, called: *Clock (Circadian Locomotor Output Cycles Kaput); Period: Per1, Per2, Per3; Cryptochrome: Cry1, Cry2; Bmal1 or ARNTL (Brain and Muscle ARNT like protein 1); Casein kinase Ie: CkIe and Rev-Erb (orphan nuclear receptor gene-related to Retinoic Acid).*[69] These genes play crucial roles in the central circadian molecular clock mechanism and in the peripheral circadian oscillators present in different tissues and organs.[70] In mammals, the central molecular clock is in the SCN of the hypothalamus[71] (although it is worth mentioning that within the evolutionary scale, in most amphibians, fish, reptiles, and some birds, the pineal gland plays this same role), while the peripheral oscillators are distributed throughout the body.[72]

The clock operation involves the interaction of positive and negative signals that regulate the rhythmic transcription of clock genes. The expression of these genes is governed by two transcriptional activation/repression loops. The positive signaling loop is controlled by *Clock* and *Bmal1* genes that dimerize in the cytoplasm to enter the nucleus, where they bind to and activate the transcription of other clock genes, such as *Per* (*Per1-3*) and *Cry* (*Cry1* and *Cry2*), through the formation of protein complexes. On the other hand, the negative signal loop is regulated by the *Per* and *Cry* genes. Subsequently, the PER and CRY proteins accumulate in the cell nucleus during the night, where they inhibit the activity of the *Clock*/*Bmal1* complex, thus stopping the transcription of the signals, *Per* and *Cry* themselves.[73] This negative feedback leads to rhythmic oscillations, and it is for this reason that the *Clock*/*Bmal1* complex is attributed to the regulation of gene expression of the circadian cycle. In addition to controlling the internal clock, this complex also regulates genes known as "*clock-controlled genes*" (CCGs), which are influenced by the circadian rhythm.[74,75] Some examples of these genes are c-*Myc*, cyclin D1, and *Wee*1, which play a crucial role in cell cycle regulation. To understand the circadian machinery at the genetic level, double hybridization experiments were performed in yeast, where it was shown that *Clock* and *Bmal1* bind to form heterodimers that activate the transcription of certain genes by specifically binding to a DNA region where their promoter is located. This region, known as the E-*box*, has the nucleotide sequence CACGTG. In this way, *Clock* and *Bmal1* behave as positive elements that activate the transcription of the Per genes (*Per1-3*), the cryptochromes (*Cry1* and *Cry2*), the *Rev-erb* gene, and other clock-gated

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genes.[73,74] As for the CLOCK and BMALI proteins, they belong to a family of transcription factors that have functional domains of the bHLH (basic-Helix-Loop-Helix) type, and PAS (Period-Arnt-Single Minded, for the name of the three proteins that share it). These bHLH and PAS domains confer the ability to bind to DNA, in the case of the former, and to dimerize with other proteins, in the latter.[75] The precise and coordinated interaction of all the components of the molecular clock makes it possible to maintain the synchronization of internal circadian rhythms with environmental signals, the main cycle being light and dark.[76] The influence of these biological processes directly influences sleep-wake cycles, metabolism, immune response, and hormonal regulation, among others, ensuring that biological processes adjust properly to environmental conditions (Figure 2).[76]

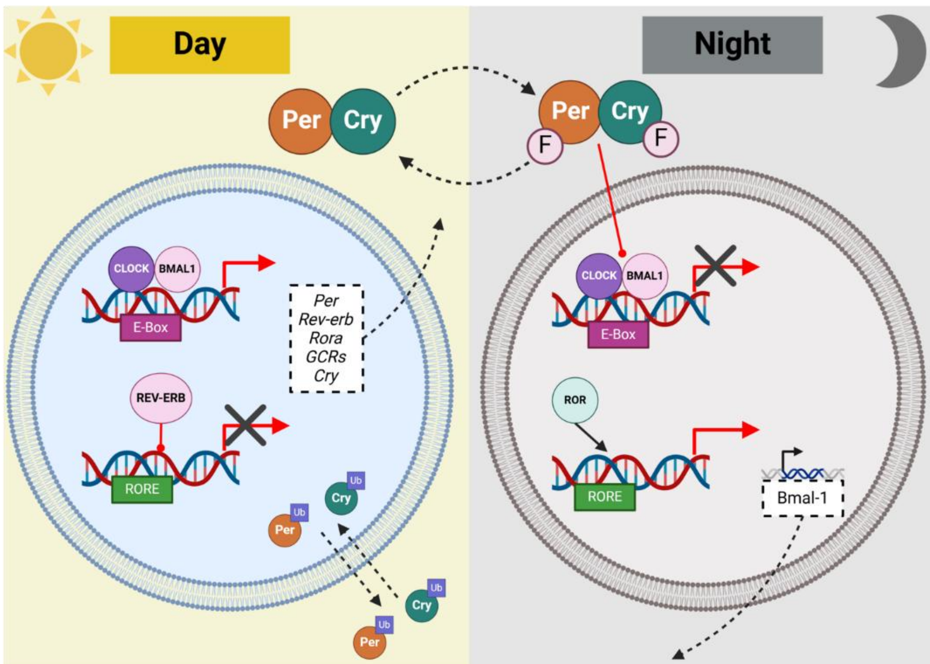

Figure 2. Circadian rhythms are controlled by molecular clock genes, such as *Clock, Bmal1, Per, and Cry*, which operate in transcriptional and translational feedback loops (~24 h). The CLOCK/BMAL1 complex activates the transcription of genes like *Per* and *Cry*, whose protein products inhibit this complex, generating rhythmic oscillations. These mechanisms synchronize biological processes such as the sleep-wake cycle, metabolism, and DNA damage repair, aligning them with light-dark cycles and ensuring temporal homeostasis. Software *BioRender*, 2021.

8. Hierarchical timing system

Circadian rhythms, being genetically encoded by a molecular clock, are present in all cells that generate an internal timing of ~24 hours in the absence of external signals.[69] Throughout the evolutionary history of the *phyla*, their molecular clocks have been organized in a coherent and hierarchical system directed by a central or master clock and consequently towards peripheral clocks directed by the former.[70] This can have different locations depending on the species, for example, in mammals it is in the SCN, in crustaceans and insects in the retina, in most fish and birds in the pineal gland, and

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even in plants that do not have a proper central clock, they have specific structures such as leaves, stromal cells and meristem cells, which coordinate their rhythms. The common characteristic of the central clock in most vertebrates, particularly in mammals, is that they form a highly unified network. This central clock is the only one that receives light input from the retina and is synchronized with the solar day.[77,78] This information is passed to peripheral clocks through endocrine and systemic signals. The characteristics of central neurons and those of peripheral tissues are that they share the same molecular architecture and the ability to generate sustained circadian rhythms; however, a key difference between master and peripheral clocks is that the former has a high degree of intercellular coupling.[79] In addition, many other clock genes and regulatory factors have been identified that contribute to the complexity and precision of the circadian clock. It should be noted that precisely because of this characteristic, the exact composition of clock genes may vary between different species, but the main function of regulating circadian rhythms is conserved. In central clock neurons, there is a high degree of intercellular coupling, forming a neural network that is resistant to phase disturbances of internal signals, while the phase of peripheral clocks is susceptible to adjustment from the central clock through circulating hormones and other metabolic signals, as well as through systemic changes such as body temperature.[80] This network ensures that the master clock faithfully maintains intrinsic ~24-hour synchronization by maintaining temporal coordination with the external solar cycle, whereas peripheral clocks adapt to reflect the metabolism of the tissues in which they function.

9. Conclusions

The evolution of life on Earth is deeply linked to the interaction between geological, chemical changes, and solar radiation. UV radiation provides the necessary energy for the formation of complex molecules. Subsequently, with the emergence of the first photosynthetic organisms, oxygen levels increased, and the formation of the ozone layer was crucial for protection against UV radiation and the evolution of more complex life forms. Cryptochromes, which evolved from an ancestral enzyme responsible for DNA repair, are blue/UVA light receptors and play a vital role in the interplay between blue light perception and circadian rhythms, reflecting an early evolutionary adaptation to solar light cycles. Photoreceptors, present in both animals and plants, have evolved to detect light and convert it into electrical signals, facilitating functions ranging from vision to the regulation of circadian rhythms. These circadian rhythms, encoded by a genetic molecular clock, are present in all cells and therefore in all organisms, generating an internal cycle of approximately 24 hours. In most vertebrates, this system is hierarchically organized by a central clock that has a different name depending on the species and location in the nervous system; for example, in mammals, it is the suprachiasmatic nucleus that synchronizes with daylight and transmits this synchronization to peripheral clocks through endocrine and systemic signals. The conservation of clock genes across different species underscores the evolutionary importance of regulating circadian rhythms for anticipating environmental changes, temporal homeostasis, and the regulation of essential biological processes such as DNA repair.

10. Conflicts of Interest

The authors declare no conflict of interest.

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