

The Diel Hypothesis and Theory of Evolution

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ABSTRACT

Hypothesis: The light/dark oscillation produced by the sun and rotating earth and the change in the period of that oscillation have played a more pivotal role in the evolution of life than the absolute passage of time. The diel theory of evolution suggests that non-organismal chemical evolution may explain much of what has been regarded as organismal biology heretofore. The diel theory may explain the origin of first life, the strict separation of mitosis from sex, the trend in evolution toward complexity, and the trend in evolution toward bigger body size. It also suggests reasons for the great oxygenation event, the evolution of multicellularity, the Cambrian Explosion, and the Sabbath. If true, every study ever done in biology and in chemical evolution more generally needs to be reconsidered in a new light (that keeps going off and on).

IT GOT LATE EARLY

Every organism, probably every cell, and perhaps every chemical reaction inside of every cell has a diurnal rhythm. I suggest that a similar diurnal rhythm existed at the surface of the ocean where I imagine life first evolved. A similar case can be made if life began in a tide pool or lake (1) but perhaps not if we can trace our lineage all the way back to a hydrothermal vent (2). Serious questions have arisen and remain unanswered for the latter hypothesis (3).

A rich organic layer on top of the ocean, which started in part from methane and other molecules seeping from vents and then building up by redox reactions occurring between the gaseous atmosphere and the liquid ocean, may have existed very early on (4). Together with light, and perhaps especially UV light, mineral catalysis from rocks in near-shore waters may have produced an increase in the complexity of early organic molecules (5,6,7). From there Prigogine's autocatalysis ideas seem compelling (8). A variety of plausible steps have been proposed for prebiotic evolution of specific metabolic pathways (9,10,11).

What has not been much appreciated however is that the prebiotic reaction mixture must have fluctuated between day and night (12,13,14,15,16,17,18,19, but see 20!). Drying cycles, temperature gradients, and temperature fluctuations have been studied, for example, early types of polymerization may have occurred in the intertidal due to drying cycles (21).

The composition of the air at the ocean's surface is in flux as chemical reactions in the ocean produce an exchange of gases with the atmosphere. Heat produces more mixing of air, so this localized exchange would not be expected to slow chemical reactions as much during the day as at night. Wave-producing wind also follows a diurnal cycle, especially near coastlines where chemical inputs come from rivers and rainwater runoff (22).

Chemical reactions occur about twice as fast for every increase of 10 degrees centigrade, so even if most reactions were common to both day and night near the beginning of earth time, these reactions would have occurred more quickly during the day as the temperature fluctuated. Light and temperature gradients at the surface of the prebiotic ocean would have also formed during the day (23). It is worth noting in this context that temperature fluctuations would have gotten more dramatic as the days got longer, from perhaps five hours at the beginning to our current 24 (24).

Further along in time, but still before any organisms evolved, light-dependent reactions appeared and probably came to dominate the prebiotic ocean. UV and visible light reactions would have helped warm the prebiotic organic layer and made the temperature fluctuation between day and night even greater (25).

Thus, whatever was happening in the ocean during the day must have been very different from what was happening at night. The modern migration of organisms that takes place up and down the water column near the surface of the ocean each day reflects this history (26).

If the evolution of life was driven by the diurnal cycle, then its history may be better measured in the number of days that pass (diel time) rather than in absolute earth time. Diel time suggests that more of our evolutionary history took place when days were shorter. Although much accounting for changes in day length over time still needs to be done (27), the first half-billion years was 11% of absolute earth time but perhaps 20% of the total number of earth days. The change in the length of the day was also more rapid early in earth's history.

There was also a long period of time before the great oxygenation event during which organismal and non-organismal chemical evolution probably cannot be distinguished by genetic methods. It may be difficult to determine exactly when organismal evolution began to dominate inheritance, but the passing of days and the lengthening rotation of the earth may continue to play a role in evolution in ways we are only beginning to understand (28,29). The diel hypothesis also has implications for space travel and the probability of extraterrestrial life (30).

ORGANISMS ARE THE CLOCK

Diurnal rhythms in metabolism and ontogeny are ubiquitous (31,32). However, the earliest organisms had no clocking mechanism to mark the days (33,34). They still had diurnal rhythms, but these rhythms were driven by metabolic reactions that occurred during the day. Endogenous timers evolved numerous times, perhaps being lost and regained in some lines.

I argue that these endogenous timers are diel in nature rather than circadian because they do not schedule anything during the course of the day so much as predict the passing of a single day and perhaps more specifically the passing of a single night. The functions of the diel timer apart from a morning wakeup call are derived (35,36,37).

Gene knockout or knockdown experiments, including those that target multiple genes, suggest that diel timers are not all that critical for normal ontogeny, especially if organisms are kept on a proper light/dark cycle (38,39,40,41). A nematode worm that has evolved in the dark does not appear to have a diel timer as such but nevertheless has not escaped its diel origins (42,43).

Organisms that evolved under the constraints of a diel ocean and atmosphere do not need a circadian clock because they *are* the circadian clock. Everything about our biology is based on the light/dark cycle, and to recapitulate that in an internal clock would be to remake the organism inside the organism. This may be compared to a search for the homunculus in the brain. There is no more need to have a circadian clock inside a circadian clock than there is to have a controller inside a controller. A body may have needed help resetting once in a while, for example on a cloudy winter day, especially as organisms evolved away from a dependence on the prebiotic ocean, and hence endogenous diel timers (44).

ORGASMAL EVOLUTION

Most or all organisms react to an artificial dose of UV light by having sex some hours later even in cases where artificial mutagens or energetic stressors will not cause such a response (45,46). This may be a direct reflection of chemical reactions already present in the prebiotic ocean (hereinafter "soup" though the atmosphere was also part of the reaction mixture). The vast array of biological molecules that interact with UV light also suggests its importance in our history (47,48).

Nucleic acid polymers (strings of nucleotides and perhaps other molecules; NAPs) found a stable place in the soup for many reasons, including for example the ability to capture light and store energy, but I want to emphasize two in particular: First, they could store information to direct their own replication and second, together with UV light, there was an efficient way to generate sequence diversity (49). The metaphor in this dichotomy between identity and diversity for the evolution of modern forms is quite powerful. Diversity-generating mechanisms and replication mechanisms are always present together but also are always separated in space and time.

At the molecular level, replication of NAPs and recombination of NAPs always occur independently. A pattern of mitosis to preserve identity and homologous recombination (transformation in archaea and bacteria and meiosis in eukaryotes; see also "sex") to generate diversity is common to all organisms (50,51). For example, multicellular organisms use mitosis to generate multiple cells but rather alternative splicing and other types of recombination to generate cell diversity. Mitosis has its roots in the synthesis and replication of complex molecules during the day while sex began as degradation, especially at night. A French phrase calls orgasm "the little death."

When double stranded DNA cells produce gametes, replication precedes recombination as life precedes death and night follows day. In fertilization, replication follows recombination so that a return to order follows a randomization step. It occurs that if replication and the generation of diversity could somehow proceed as one on the molecular level, then cells would probably generate only two gametes—similar to the mitosis pattern--instead of four.

The primordial diversity generator probably used UV light to cause changes in NAPs, which in turn led

to their partial degradation (49). Degradation products then formed a new sequence in large part due to the chemistry of the NAP polymers themselves. Homologous recombination evolved from this milieu of already-reorganizing polymers. There may have also been a time in evolution when single celled organisms simply lysed on competence in order to undergo homologous recombination in a manner somewhat reminiscent of, and for the same purpose as, spawning. This may have given way to clustering of like organisms, and this step may have distinguished the first of what we call a species derived by organismal evolution (52,53). Clustering apparently then gave way to transformation as the primary mode of sex in early forms.

The primordial replicator also used light but more likely to preserve identity than to change it (54).

Mitosis and sex do have one feature in common: They both tend to happen after dark. Asexual reproduction most often occurs at night (55,56). Even complex animals that take many days to develop to maturity do mitosis in a dark egg or womb. Our branch of mammals lost the ability to correct replication errors with light while evolving an exaggerated placenta (54,57).

Accumulating chemical bonds from UV light could only happen during the day, but modern recombination of nucleic acid strands may be more easily done in the dark away from interfering light. One type of modern bacteria reaches competence six to eight hours after UV exposure (58). The more complex, derived protists probably needed at least one entire energy-gathering day to have a proper ontogeny anyway, and sex at night may have been more advantageous because it did not interfere with the rest of the day's activities. Morning would also appear to be an ideal time to perform the sex act if homologous recombination occurs overnight (59).

The evolution of identity generation and the evolution of diversity generation must be told as one story. It may not be possible to tell that story with organismal evolution because both identity and diversity generation imply multiple individuals. The evolution of identity and diversity may be better left to explain observations at the species level (60). This suggests, unfortunately, much of evolutionary theory to this point has been about trying to determine which came first, the chicken or the egg.

A JUST-SOL STORY

An evolutionary hypothesis or theory often comes with a compelling but errant just-so story that receives more attention than the theory itself, even when the theory does not really hinge on the details of that story (61). For example, I choose to highlight the possible role of indoles because that is what stimulated my interest in early evolution (62,63). However, if most of what I say about indoles proves to be wrong, it would not seem to change much about the diel theory of evolution. I could use another of the many light-gathering molecules at an organism's disposal to tell essentially the same tale. My just-sol story does turn on the idea that fluctuations in light and temperature occurred in the prebiotic ocean and atmosphere. It strongly suggests a rich proto-metabolic soup full of complex, organic proto-biological molecules.

In the beginning, the earth was spinning quickly. Days lasted only a few hours. Early chemical evolution consisted of simple reactions whose energy barriers were not high compared to ambient heat. Fluctuations in heat and light were already occurring in the oceans and atmosphere due to the solar day, but geochemistry was also driven by non-diurnal heat leftover from earth's accretion. As days got longer, they also got hotter, and nights were increasingly cold.

As the more spontaneous reactions played out, daytime chemistry began to dominate. Simple light-dependent reactions evolved early on and would soon come to be the energy source for all proto-metabolic activity in the ocean. Boundary layers and chemical gradients formed at the surface of the ocean. During the day there was a gradient of light strongest at the surface and weaker with depth.

A myriad of light reactions occurred during the day near the surface while at night less happened, and what did happen was based primarily on the leftovers from the daytime because that's what dominated the soup. Some substrates diffused to the top, where they were used, and products diffused down after being produced in the light. Also, as the soup began to take on a hydrophobic character, an aqueous/organic boundary layer emerged.

As the complexity of reaction products, and therefore reaction substrates, increased, so too did their interconnectedness. The product of one reaction served as the substrate for another. These interconnected light and dark reactions were the earliest version of what we might now call anabolic and catabolic metabolism, respectively. However, only simple polymers were present. Among the molecules that found a stable position in the soup were indole rings that gathered light, and even these were simple compared to modern biological indoles.

Dark reactions initially occurred during both the day and the night and both at the surface and at depth. In some cases, as the complexity and interdependence of reactions grew, the dark reactions--dependent already on light reactions for substrates--started to use indoles and other light-sensitive molecules in situations where light actually did not favor the reaction.

Then indoles and other molecules started to become catalysts somewhere in their own chemical cascades. Other types of molecules began to catalyze their own polymerization, and self-replicating molecules soon dominated the soup. However, the vast interdependence of the reactions did not change. Light-gathering molecules still harnessed all the energy, which was used by both types of reactions in the form of a proto-ATP that had become a plentiful product of one common type of light reaction. Still, even the more complex, self-replicating molecules that had been formed after a long day of light reactions were degraded at night.

As the days got longer, longer polymers and increasingly complex aggregations of molecules formed. Compartmentalization protected polymerization from interference from UV light and so became a ubiquitous innovation. Free radicals became more of a problem in a compartmentalized space, and indoles came into their own as free-radical scavengers.

What we might call life emerged during this time. Proto-cells of various types even had rudimentary kinds of competition and symbiosis. Of course they were all degraded at night by proto-viruses anyway, entering back into the vast interdependent soup. Who won and who lost was as much determined by resulting breakdown and recombination of products as this new kind of organismal competition that happened during the day. DNA began to replace RNA as the primary polymer used for information storage, replication, and recombination.

As the days got longer, organisms started to live through the night by sinking and spreading in the water column. Positive phototaxis in the morning made this possible. Proteins first evolved to move the chemistry of indole rings inside the cell, and many modern proteins still use light to do their work, reflecting this history (64,65,66). Tryptophan embedded in an amino acid polymer came to be the modern way to do the work of prebiotic indole rings. And there was life by anyone's definition.

Organisms began using the nighttime soup to prepare for morning. However, they still tended to die at night for lack of energy, and life was still arranged around an even number of days, just not always one day anymore.

Exchange between organisms and the soup evolved toward increasingly simple substrates. Metabolism moved from the prebiotic ocean into the organism. Lines dependent on the soup for complex products went extinct. Some organisms used the circadian pattern of one indole's formation in order to predict the length of the night and wake up on time (67). Achaeta carpeted the intertidal. And the days got longer. And hotter.

ON THE LACK OF POSITIVE FEEDBACK

The origin of the great oxygenation event is unknown (68). The most popular theory has it that oxygen from photosynthetic bacteria slowly rusted most of the iron out of the ocean, which then caused a population explosion. However, this theory has empirical difficulties, and the usual emphasis on light reactions seems unwarranted (69).

Another possibility is that when the same organisms producing oxygen also began to fix carbon in a unique way, a positive feedback loop was created, and perhaps this feedback system is already known. The crucial step may have come when carbon and/or nitrogen fixation became directly regulated by--as opposed to just dependent on--light reactions (70). This simple hypothesis about one or a few gene mutations makes sense in the strobe light of evolution if organisms are incorporating more and more of a metabolic soup already on a diurnal rhythm. When one or a small number of species could use the most important dark reactions for their own agenda instead of the general welfare of all photosynthetic organisms, other photosynthetic species were transformed by this newly minted genetic material or went extinct.

And Eukaryotes emerged. And there was not much soup left (71). And the nights got longer. And colder.

SWEET SPOTS IN DIEL TIME

There were bottlenecks and extinctions to be sure, but also an increase in diversity.

The intertidal zone was a harsh place where it was difficult to string together successful mutations to make it a habitable niche. However those organisms that did overcome this hurdle found a big advantage because they could live there, or hide there, or eat there.

Besides the most important oscillation in the intertidal, waves crashing ashore on top and undertow beneath, slower oscillations occur. High and low tides happen regularly, in most places twice in just over a day. Any organism that could predict these highs and lows could gain a clear advantage. However circadian clocks were unable to evolve into a niche based on a different time. They count to one, not 1.04.

There is another, even slower oscillation in the changing tides. Every one-fourth of a lunar month or lunar week, the tides change from getting more extreme to getting less extreme or vice versa. The

lunar week has changed over time mostly due to tidal locking between the moon and earth. Days have gotten longer but so have the weeks as the moon's orbit gets longer.

During most of evolution, including today, the lunar week has not correlated with the solar day except perhaps at some very long time scale. However, at times during the procession of the moon's orbit, sweet spots occurred such that the lunar week could be predicted by the solar day. It is possible that a four day sweet spot occurred early in earth's history, perhaps before watery oceans. In a four day sweet spot, the tides would have gotten more extreme one day and less extreme the next. On some shorelines, this diurnal change in tides might have even synchronized with morning or evening. An organism could conceivably evolve a diurnal lifestyle in the intertidal during such a sweet spot. However, it seems likely that eight, twelve, and perhaps other sweet spots would have passed very early on in history. It becomes more difficult to see how simple organisms could evolve a diurnal lifestyle in the intertidal even during such sweet spots as the number of days per lunar week increased. Nevertheless, the many sweet spots that followed could have added a kind of saltatory nature to evolution.

But where were we? Ah yes, eukaryotes. The tides remained inconsequential in biological-circadian-clock evolution for almost another billion years. Then, 1.5 billion years ago, plus or minus, eight solar days came very close to the lunar week. If an organism could count to eight, a rich unexploited food source would become available. Single-celled circadian clocks could not do it; it was just too many days. However, organisms with a clonal cluster stage in their life cycle fared better.

Multicellular eukaryotes may have emerged under this selective environment. They found success exploiting the intertidal as a source of food during high tide and retreating toward or into the subtidal during low tide. They simply changed their behavior once per week. One of their first adaptations, positive phototaxis, mirrored that of early life (72). Multicellular creatures thus acquired a synodic pattern, and most modern forms retain some vestige of this pattern. The Sabbath may be a zeitgeber for the ancient, internalized human synodic week (73).

(It will be of interest to see how diel rhythms (and endogenous diel timers) and synodic rhythms (and endogenous synodic timers if any) interact in modern organisms, including those that still exploit the intertidal, since the tides no longer align with the days (74,75,76).)

But diel time still plodded along. In as little as 25 million years the strategy of exploiting the intertidal started to fail because the two clocks were no longer in synch. Weeks lasted between seven and eight solar days as they do now. Multicellularity persisted in many forms, but you would not say flourished.

Another 800 million years or so passed, and another sweet spot occurred. This time there was no alignment of the tides with the solar day but rather seven solar days came to be as long as the old eight-day cycle. Thus, many ontogenetic cycles of multicelled creatures came to once again align with the day. There is usually pressure that favors faster ontogeny, so shortening the week from eight to closer to seven days happened easily.

The main advantage of the new sweet spot was simply that the new seven-day week matched up well with circadian ontogeny, which benefited many multicelled creatures in and out of the intertidal. And the Cambrian blew up.

SIZE AND COMPLEXITY MATTER

The story of evolution has always been about energy from the sun creating order in a non-equilibrium system. However, non-equilibrium systems need fluctuations and perturbations to drive them away from steady states. The diel hypothesis highlights the most important fluctuation in the environment, the light/dark cycle produced by the sun and rotating earth. The lengthening rotation of the earth also provided a perturbation to the system, albeit a slow one.

The premise is that longer days facilitated the presence of an increasingly complex set of metabolic reactions in the soup both during the day and at night. Thus, the diel theory of evolution suggests a possible explanation for the apparent increase in complexity during evolution. Life emerged when the day got long enough to construct entire individual organisms. Meiosis emerged when the day was long enough to eat, find conspecifics, and reproduce. It even seems possible that the recent emergence of *Homo sapiens* happened more or less as soon as the days were of sufficient length. A similar line of reasoning suggests a partial explanation for increases in body size over time (77).

Together these observations suggest an important role for the lengthening day in speciation. Organismal evolution happens quickly compared to changes in day length. However, changes in day length still drive the overall size and complexity of organisms in derived niches. Lamarckian evolution occurs since the characters that get used are the same ones increasing in complexity, and this change is not due to organismal evolution in the following sense: The organisms evolving may have tried the same innovation many times, but that innovation only succeeded when the days got long enough (78). Thus, the diel theory of evolution unifies Darwin and Lamarck (79).

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