

THE PALIRRHOTROPHIC ORIGIN OF ENERGY METABOLISM

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Abstract. It is proposed that the earliest cellular organisms relied upon a novel type of energy transduction termed palirrhrotrophy, which generates a high-energy 'currency' chemiosmotically by exploiting the rhythmic variations in salinity which occur in the estuarine environment. Calculations based on estimates of contemporary chemiosmotic transduction efficiency suggest that such a mechanism could produce usable energy in high yield. The minimum polypeptide requirement for palirrhrotrophy compares favorably with that of a fermentative pathway. It is suggested that palirrhrotrophic organisms exist today but are difficult to detect.

The source of amino acids and other organic compounds for the earliest organisms can be accounted for by spontaneous abiotic processes. However, there is no evidence for the formation or accumulation of substantial quantities of high-energy compounds, such as ATP, under prebiotic conditions. Because the hydrolysis of ATP is required by virtually every biological function, it appears unlikely that cellular evolution could have progressed beyond a very primitive stage before a means of generating such an 'energy currency' in quantity had been developed.

Rudimentary versions of the present-day chemo- and photo-trophic metabolisms have most frequently been offered as candidates for early energy economies. Neither of these alternatives is satisfactory as the first energy economy, however, as neither can be ultimately reduced to a one-step process. As Horowitz (1945) has pointed out, multi-step metabolisms cannot be supposed to spring into existence *ex nihilo*, but must be evolved from a simple one-step reaction. Fermentation metabolisms observed today employ many steps and are extremely difficult to reduce. Perhaps the simplest known phototroph, *Halobacterium halobium*, can generate ATP through a two-step sequence: a pigment protein, bacteriorhodopsin, drives H⁺ ions into the cell, and a second protein complex couples the outward efflux of H⁺ ions to the phosphorylation of ADP (Racker and Stoeckenius, 1974). Because the two phototrophic steps are vectorial reactions proceeding in opposite directions, it is difficult to envision how phototrophy might be reduced to a single step.

I propose that phototrophy evolved from an earlier one-step metabolism which I term palirrhrotrophy (Gk. *παλιρροια*, tide). Since the appearance of the oceans, the energy of the earth's rotation has been gradually dissipated through the ebb and flow of the tides. Along the greater part of the shoreline, this energy has only been available as mechanical motion, but in the estuaries of freshwater rivers and streams, the rhythmic exchange of fresh and salt waters has offered a source of potential chemical energy. A sessile organism in this environment experiences a fluctuation in external sodium concentration from almost nil (low tide) to 460 millimolar (high tide) (Manglesdorf, 1967). Today, tides occur approximately every

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twelve hours, but the evidence of the stromatolites suggests that in protobiotic times, tides were higher and more frequent owing to the faster rotation of the earth and revolution of the moon (Cloud, 1968).

Chloroplast fragments can phosphorylate ADP in darkness in response to an abrupt increase in external pH (Jagendorf and Uribe, 1966). A coupling protein in the membrane harnesses the release of H^+ ions to the formation of a high-energy bond, converting the free energy of a concentration gradient into biologically useful energy in the form of ATP. Although H^+ ions appear to be the driving force of chloroplast and mitochondrial phosphorylation, artificially high Na^+ and K^+ gradients across the erythrocyte membrane also stimulate phosphorylation (Garrahan and Glynn, 1967). Thus estuarine organisms operating on this principle could use the sudden depletion in external ion concentration at low tide to couple Na^+ (or Cl^-) efflux to phosphorylation or some functionally analogous process. If all the internal Na^+ ($460 \mu\text{mole ml}^{-1}$) were coupled at a ratio of $2Na^+/ATP$ (analogous to the $2H^+/ATP$ postulated for mitochondrial transduction (Mitchell, 1967)), a palirrhrotrophic organism could generate as much as $230 \mu\text{mole ATP g}^{-1}$ per ebb tide. Respiring organisms produce about $6ATP/(O_2 \text{ respired})$, or 0.27 mole ATP per liter of oxygen. Thus the maximum ATP production of a palirrhrotroph per tide is equal to an hour's respiration at the rate of a pigeon ($830\text{--}1100 \mu\text{l } O_2 \text{ g}^{-1} \text{ hr}^{-1} = 220\text{--}290 \mu\text{mole ATP g}^{-1} \text{ hr}^{-1}$) or a day's respiration at the rate of *Boa constrictor* ($3\text{--}30 \mu\text{l } O_2 \text{ g}^{-1} \text{ hr}^{-1} = 1\text{--}8 \mu\text{mole ATP g}^{-1} \text{ hr}^{-1}$) (Altman and Dittmer, 1971). Producing ATP in intense bursts during tidal transitions, the palirrhrotrophic metabolism can temporarily supply ATP at very high rates, or at moderate rates with a low coupling efficiency.

Too little is known about the mechanism of coupling proteins for us to estimate the probability of one arising randomly, but the size of modern proteins provides some indication of relative complexity. Na, K -dependent ATPase, which appears to couple ion flux to phosphorylation under special conditions (Garrahan and Glynn, 1967), is composed of two polypeptides, molecular weight 93000 and 47000 (Hokin, 1974). Since this is a specialized protein which drives sodium and potassium fluxes in opposite directions across the membrane, perhaps a more primitive and less discriminating protein might have a lower minimum molecular weight. For comparison, the alcoholic fermentation of glucose requires eleven separate enzymes whose total weight exceeds 1000000 (Lehninger, 1970).

Because phototrophy requires a light-powered ion-pump in addition to a coupling protein, it must necessarily be more complex than palirrhrotrophy. The ion-pump unit in *Halobacterium halobium* is a relatively small protein (MW 26000) conjugated with a pigment (Oesterhelt and Stoeckenius, 1971) which may require enzymatic synthesis. Evolution of an independent pump to create ion-gradients rather than passively exploiting tidal transitions would confer several advantages. Phototrophic organisms would no longer be restricted to estuarine areas, but could colonize the entire shoreline. Whereas palirrhrotrophs only produce energy in intermittent bursts twice daily, phototrophs could generate ATP at a more even rate during daylight. Furthermore, palirrhrotrophs are necessarily 'poikilohalic', tolerating widely fluctuating levels of cytoplasmic salinity which interferes with macromolecular structure.

Palirrhrotrophy is a possible evolutionary 'stepping-stone' whereby an organism with very restricted synthetic capacities can survive and gradually evolve into a self-sufficient phototroph. Possibly, it is the only such stepping-stone. If this is so, then one can draw some interesting corollaries regarding preconditions for biogenesis. Tides presuppose that a rotating body is under the influence of an external gravitational field. If the external field is weak, as is the case for Mars and Jupiter, substantial tides cannot occur. If it is too strong, as is the case for Mercury and the moon, then rotation is arrested, leading to thermal extremes incompatible with life. Palirrhrotrophy also presupposes the existence of land which serves both as a catchment for fresh water and a substrate. Without land, tides are biologically useless, yet if there is too little open ocean there will be no large tides.

Fortuitously, all these preconditions are met by the earth. The lunar component is twice the solar today (Defant, 1958); in earlier times it was even stronger owing to the moon's faster revolution. Although tidal friction has considerably reduced the rate of the earth's rotation, our diurnal period is not so long as to give rise to intolerable thermal extremes in most areas. The earth has land areas which are relatively concentrated into a few large continents, permitting both freshwater rivers and oceanic tides. The precise alignment of continents in earliest times is not clear, but fossil stromatolites testify to the existence of shores and tides. If we enter these preconditions into our calculations of the probability of life occurring elsewhere in the universe, it will be necessary to revise our previous estimates downwards. Perhaps the possibility of coming into contact with another biogenic region is exceedingly remote.

If palirrhrotrophy is a feasible means of energy transduction, then one might well ask why no such organisms exist today? Perhaps the difficulties inherent in the process made them uncompetitive, and they have long been extinct. Another possibility is that they still exist but have not been identified. Many of the more exotic micro-organisms were first detected because their metabolism caused highly visible changes in the environment, such as the corrosion of pipes, the accumulation of sulfide, or the depletion of nitrate. Palirrhrotrophy works no obvious change in the environment whatever. Moreover, palirrhrotrophs only function in a dynamic environment of ion-concentration transitions, whereas plants and micro-organisms are usually cultured by investigators in constant media. Some estuarine plants may be facultative palirrhrotrophs, transducing tidal energy to supplement their energy supply, but it will be difficult in these cases to distinguish increased growth due to palirrhrotrophy from nutritional effects. Estuaries do have high levels of ecological productivity, but this may be due to other factors (Odum, 1974). A palirrhrotroph would be of such interest to bioenergetics and exobiology that I urge a closer examination of the responses of estuarine organisms to salinity transitions.

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References

- Altman, P. L. and Dittmer, D. S. (eds.): 1971, *Respiration and Circulation*, Fed. Am. Soc. Exp. Biol., Bethesda.

- Cloud, P. E.: 1968, *Science* **160**, 729-736.
- Defant, A.: 1958, *Ebb and Flow*, Univ. Michigan Press, Ann Arbor, p. 48.
- Garrahan, P. J. and Glynn, I. M.: 1967, *J. Physiol.* **192**, 237-256.
- Hokin, L. E.: 1974, *Ann. N.Y. Acad. Sci.* **242**, 12-23.
- Horowitz, N.: 1945, *Proc. N.Y. Acad. Sci. U.S.* **31**, 153-157.
- Jagendorf, A. T., and Uribe, E.: 1966, *Proc. N.Y. Acad. Sci. U.S.* **55**, 170-177.
- Lehninger, A. L.: 1970, *Biochemistry*, Worth Publishers, New York.
- Manglesdorf, P. C.: 1967, in *Estuaries* (ed. G. H. Lauff), Am. Assoc. Adv. Sci., Washington, pp. 71-79.
- Mitchell, P.: 1967, *Fed. Proc.* **26**, 1370-1379.
- Odum, E. P.: 1974, in *Ecology of Halophytes* (ed. R. J. Reimold and W. H. Queen), Academic Press, New York and London, pp. 599-602.
- Oesterhelt, D. and Stoeckenius, W.: 1971, *Nature New Biol.* **233**, 149-52.
- Racker, E. and Stoeckenius, W.: 1974, *J. Biol. Chem.* **249**, 662-663.