THE POSITION OF NITRATE RESPIRATION IN EVOLUTION

(Reply to F. Egami)

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(Received 29 November, 1976)

Abstract Egami's hypothesis that oxygen respiration evolved from nitrate respiration, and this from nitrate fermentation, is not accepted. The reasons are: (1) Presumably there was no nitrate before O_2 in the biosphere. (2) On mechanistic grounds, respiration (oxidative phosphorylation) is to be derived directly from photosynthesis (photosynthetic phosphorylation) rather than from any form of fermentation.

Egami, to whom we owe gratitude for his brilliant contributions to bacterial nitrogen metabolism, has now once more defended his hypothesis that oxygen respiration was preceded by nitrate respiration (Egami, 1976). His recent note is specifically directed against the present author's view (Broda 1975, a,b) that nitrate respiration developed from oxygen respiration.

One of my main arguments is that in the absence of free oxygen the presence of nitrate in the biosphere cannot be assumed. The formation of nitrate would be a most strongly endergonic process:

$$0.5N_2 + 3H_2O = H^+ + NO_3^- + 2.5H_2\,; \qquad (1)$$
$$\Delta G_0' = 134\,\text{kcal/mole}.$$

It would remain highly endergonic if the pressure of H_2 were decreased, i.e. in the transition from reducing to neutral conditions. For instance, ΔG would still be as much as 114 kcal/mol at $p_{H_2} = 10^{-6}$, and 94 kcal/mol at $p_{H_2} = 10^{-12}$. Egami now argues that "thermochemical calculations have little significance" and points to the endergonic synthesis of aminoacids.

Indeed with external energy, e.g. from electric discharges, endergonic reactions may, within certain limits, be forced; see Miller's (1953) classic experiments on aminoacid production. Yet this fact does not entitle us to postulate the feasibility of the endergonic build-up of a strong oxidant (nitrate) in reducing conditions, i.e. in the presence of large amounts of sulfides and of ferrous iron, and in the absence of O_2.

In an alternative line of arguments, Egami starts from the assumption that the primeval atmosphere did contain O_2. However, practically all geologists and biologists agree that before the advent of plant photosynthesis the O_2 content of the atmosphere was minute, and therefore not effective thermodynamically and kinetically (see Berkner and Marshall, 1976). Van Valen (1971), quoted by Egami, was apparently misunderstood; Van Valen did not commit himself to an appreciable O_2 level in the primeval atmosphere at any time. Egami proposes that nitrate gradually accumulated even in an atmosphere

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containing little O_2 only. But this would require high stability of nitrate, in presence of an enormous excess of solid, liquid and gaseous reductants and over geological periods. Such stability would have to be experimentally demonstrated to be believed. Even Rambler and Margulis (1976), who like Egami favour the precedence of nitrate respiration before oxygen respiration, admit that the synthesis of nitrate presupposed production of oxygen by plants (blue-green algae).

Most damaging to Egami's (1974, 1976) scheme

fermentation → nitrate fermentation → nitrate respiration → oxygen respiration

is its feature which he does not mention explicitly, namely that photosynthesis has no place in it. In view of the striking similarity between electron flow, with phosphorylation, in photosynthetic and in oxidative membranes, photosynthesis must be included into any viable evolutionary scheme. According to the 'conversion hypothesis' (Broda, 1975a), photosynthesis and respiration followed one from the other. In Egami's scheme no evolutionary connection of photosynthesis and respiration is apparent.

In the most probable form of the conversion hypothesis the evolutionary path

fermentation → bacterial photosynthesis → plant photosynthesis → oxygen respiration → nitrate respiration

is proposed, i.e. oxygen respiration developed (in various groups of prokaryotes in parallel) after the blue-green algae had provided O_2 An alternative sequence

fermentation →
bacterial photosynthesis →
plant photosynthesis ↗ oxygen respiration
plant photosynthesis ↘ nitrate respiration

would also agree with the conversion hypothesis, but appears less likely, as all known nitrate respirers are facultative aerobes, i.e. oxygen respirers. The reverse is, of course, not true.

In the present author's view, nitrate fermentations, i.e. fermentations with nitrate as electron acceptor, are relatively late and relatively unimportant offshoots of ordinary fermentations, with nitrate instead of an organic compound as electron acceptor (Broda, 1975b).

References

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