Multi-author Review

Ecological implications of metabolic biochemistry

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Ecological implications of metabolic biochemistry: Elephant parts and the third secret of life

Introduction

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John Godfrey Saxe's poem[5], based on a famous Indian legend, tells us of six men, 'to learning much inclined, who went to see the elephant, though all of them were blind'. Biologists study life in very much the same way that the blind men in the poem grope at different parts of the elephant. The conceptual barriers built up between the various areas of biological research have resulted in an elephant that is different things to different people. To the biochemist holding the trunk, the elephant is a snake, while to the organismal physiologist with arms around the leg, the elephant is like a tree. The ecologist, feeling the body, thinks it is a wall. Common sense tells us that the elephant is no more its trunk than it is its leg; life is not 'better' studied with one approach than with another. Thus, although a more detailed analysis of the trunk or leg (perhaps made possible by technological advances) would reveal more about the nature of these parts, it will certainly not lead to new insights into the nature of the elephant itself.

Much of today's research in metabolic biochemistry is done with bacteria, yeast, and rats; the goals do not differ much from those of Meyerhof and Warburg in the 1920's and 30's (the elucidation of reaction mechanism and metabolic pathways) and Monod and Koshland in the 1960's (the unraveling of mechanisms of enzyme regulation). Life is analyzed using the tools of chemistry and physics: the elephant is held by its trunk and described as its trunk.

This Multi-author Review of Experientia contains articles written by those interested in the nature of the elephant itself. We have defined metabolic biochemistry broadly to include not just the reactions and pathways involved in the transformation of energy, the synthesis and degradation of biomolecules, and the production of waste products, but the digestion of food and assimilation of nutrients as well. Since metabolism occurs not in structureless watery sacs, but in complex, highly organized, and functionally integrated systems, no attempt is made to create what we believe to be an artificial distinction between physiology and biochemistry. Thus, readers more comfortable with traditional categories will find that there is 'more physiology than biochemistry' in some of the articles.

In a series as short as this one, it has not been possible to be 'encyclopaedic' in our coverage of subjects. Nevertheless, we have attempted to illustrate our integrative approach to metabolism with a broad spectrum of articles, starting with the effects of the physical environment on the catalytic and regulatory properties of metabolic enzymes. Most biochemists working in chemistry and biochemistry departments seldom (if ever) wonder about enzyme adaptation to the physical environment. In his article, Somero explores the role played by enzyme properties (presumably evolved and ultimately resulting from differences in primary structure) in determining fitness to various habitats within vertical and horizontal gradients in the deep-sea. We may think of this article as one on how molecular evolution has been influenced and constrained by the physical environment.

Biochemical evolution as influenced by nutritional factors is covered in the next two articles. Martinez del Rio, Baker and Baker explore the relationships between intestinal enzyme content and dietary preferences in birds. Digestive enzymes and feeding behaviour in birds have coevolved with the plants whose flowers they pollinate and whose seeds they disperse such that these have become 'prey that want to be eaten'. In the second article on nutrition and digestion, Diamond and Hammond assess the utility of Taylor and Weibel's concept of 'symmorphosis'[6,8] by considering the evolutionary design of digestive capacities. The concept of symmorphosis has provoked considerable discussion and controversy[1-3]. The hypothesis proposes that anatomical structures and functional capacities are designed economically such that these are matched to maximum physiological loads or flux rates. Excess capacities are wasteful of space, time, and energy and are eliminated by natural selection.

The rest of the articles also deal with evolutionary design and functional integration. Metabolic fuel fluxes between organs, e.g., glucose from livers to locomotory muscles during exercise, is covered by Weber who suggests that rate-limiting steps are the ones that are most up-regulated when athletic species are compared with sedentary ones. We are led to wonder whether these are the steps that are most subject to selection.

Suarez points out that there are limits to evolutionary design from the organismal to the subcellular levels. Amongst the smallest and most aerobic vertebrate homeotherms, maximal oxygen fluxes may be limited by how large hearts can be and how fast they can beat. Only so many enzyme molecules can fit on mitochondrial cristae, and only so much cristae can fit into mitochondria. Limits to the up-regulation of functional capacities play important roles in determining the upper limits to physiological performance. It is suggested that these functional limits may be involved in determining the lower limits to body mass in birds and mammals.

Hochachka, in his article on diving in seals, calls our attention to mammals for which 'normal life' involves being under water and being (from our anthropocentric point of view) 'hypometabolic' most of the time. Thus, while at sea, breathing at the surface and becoming 'hypermetabolic' is, in a certain sense, the exception rather than the rule. Many of these same marine mammals (some marine birds and bears, as well) are adapted to long periods (months) of natural fasting. Castellini and Rea point out that these fasts form part of the repertoire of behaviours associated with annual reproductive cycles; they explore the metabolic adaptations that make long fasts possible and those that prevent the potentially terminal processes associated with starvation.

There is much current debate about the functional significance of the urea cycle in mammals. A fresh perspective is provided by Mommsen and Walsh in their review of ammonia and urea production by fishes. Although the generalization that 'fish make ammonia because it can diffuse into the water they live in' is learned by most students of biochemistry and physiology, consideration of urea production in fishes, its evolution and adaptive significance may provide insights perhaps unavailable through the study of mammals alone.

Of the contributors to this issue, only one, perhaps two, can be called ecologists (at least some of the time). True ecologists (those who work in ecology departments or publish in ecological journals), comfortable with their own special part of the elephant, hardly ever think about metabolic biochemistry and what its ecological implications may be. We hope that our articles will provoke such readers to wonder about the nature of the whole elephant as well: the relationships between enzyme properties and metabolism and where animals live, what they eat and how much they eat, what fuels they derive their energy from, how fast and how long they can run, swim or fly, and how large or small they can be.

When Watson and Crick discovered the double-helical structure of DNA, they proclaimed that they had 'found the secret of life'[7]. After Monod conceived the idea of allosteric control of metabolic enzymes, he said that he had 'discovered the second secret of life'[4]. These were, indeed, great advances in the study of molecular biology and biochemistry. Those who follow in their footsteps continue to advance these fields at a phenomenal pace. But they continue to grasp only the trunk. The time has come to move on to the rest of the elephant in search of the third secret of life.

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