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The Biology of Lipids: Integrative and Comparative Perspectives[1]

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A unifying feature of lipids is relatively low solubility in aqueous media, yet lipids embody an immensely disparate set of molecules. It can be argued that lipids represent some of the most complex biological molecules. Classes of lipids include hydrocarbons, alcohols, fatty acids, waxes, glycerides, phospholipids, and glycolipids. There are also variations on a theme within a single lipid class. Molecular species that make up a lipid class possess differences that are seemingly subtle, but these differences oftentimes have major consequences for physical properties and ultimately for biological function. The complexities of these molecules (including their composite nature, intricate structure, and daunting nomenclature) have intimidated many a biochemistry student and professor!

Not surprisingly, functional diversity is another hallmark of lipid compounds. The wide array of chemical and physical properties of different lipids allow these molecules to perform a variety of roles in biological processes. Polar lipids arranged as bilayers establish barriers to free diffusion of water and solutes, provide a microenvironment for membrane-associated proteins, and organize and maintain an interface between discrete metabolic and functional compartments. Surface lipids are integral to water balance in all terrestrial organisms. Lipids serve as metabolic fuels and signalling molecules (hormones, second messengers, and pheromones). Lipids play specialized roles in many organisms as electrical (myelin) or thermal (blubber) insulators. Surfactant lipids are essential components of the gas exchange organs of many air-breathing animals. In addition, many aquatic organisms use lipids as agents of buoyancy and as a result reap the benefits of significant energy saving.

The range of functional roles ascribed to lipids rivals the functional diversity of proteins, yet lipids are probably the least well-studied class of biomolecules. Lipids are "the Cinderella" of biological molecules, as Christian de Duve (1993) has said for the peroxisome, a relatively understudied organelle. In this case, the stepsisters (proteins, nucleic acids, carbohydrates) are not ugly but they certainly receive the most attention. Lipids seldom receive their share of credit for cell function; they are often overlooked when a responsible agent is being sought to explain some cellular phenomenon.

More researchers in comparative and adaptational biology are recognizing the significance of lipids and their potential for playing major roles in many biological processes. Therefore, we thought it appropriate to bring together researchers whose common ground is lipids, but whose work demonstrates the functional diversity of lipid molecules or lipid-based macromolecular structures. Because lipids are important at many levels of biological organization from molecule (*e.g.*, adaptational biochemistry) to organism (*e.g.*, animal behavior) our choice of symposium topic lends itself to an integrative theme. We hope to spark greater interest and appreciation for lipids in the more general audience, as well as provide timely syntheses of particular aspects of lipid biology and a broad view of lipid function.

The collection of papers that follows illustrates the diversity of lipid function in biological processes. The first half of the symposium focuses on "structural" roles of

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lipids. In these cases, the physical properties which define lipids as a class are also the key factors responsible for their physiological functions. For example, the ability of cell membranes to form a barrier to movement of molecules into and out of the cell depends on the physical state of the membrane lipids and their interactions with proteins and other membrane constituents. Epicuticular lipids of insects play a more narrow role in preventing evaporative water loss, and again the physical properties of the constituent lipids are important in maintaining a barrier to water flux.

An overview of the importance of physical properties of lipids in barriers is provided in the first paper by Gibbs. The next two papers, by Williams and Crockett, treat cell membrane function in greater detail. They address the questions of which physical properties of cell membranes are most critical for membrane function, and what is the role of cholesterol in regulation of membrane fluidity. A different example of a lipid barrier is the surfactants of the vertebrate lung. Daniels *et al.* discuss the mechanisms by which poikilothermic animals prevent lung collapse due to surface tension, despite the sensitivity of lung surfactants to changes in environmental temperature.

Lipid properties are central to non-barrier roles as well. Most lipids are less dense than water, and numerous taxa use them as buoyancy mechanisms (Phleger). Limits of space and time prevented inclusion of other examples of the importance of lipid physical properties (*e.g.*, maintenance of fluidity in depot fats of mammalian hibernators [Irving *et al.*, 1957], lipids as mediators of oxygen diffusion at low temperatures [Desaulniers *et al.*, 1996]). The defining characteristic of lipids, their physical state, is clearly the crucial factor in determining the physiological function of many lipid systems.

Speakers in the second half of the symposium discuss the variety of non-structural roles of lipids. These topics can be generally divided along the lines of lipids in energy metabolism and lipids in communication. For example, hibernating mammals need to store large quantities of lipids in order to survive months without access to food. Lipid metabolism must be tightly regulated during this period (Florant), but lipids must also be prevented from undergoing spontaneous oxidative damage (Frank). Regulation of lipid deposition and synthesis is critical in development as well. Sheridan and Kao provide a summary of recent work demonstrating the hormonal control mechanisms common to lipid metabolism across vertebrate taxa.

Lipids are involved in communication at all levels of organization. Stanley and Howard provide an integrative review of the rapidly expanding field of the comparative biology of eicosanoids and prostaglandins. The evolutionary and ecological importance of these important signalling molecules are emphasized. Lipids also act in communication between individuals. Schal *et al.* discuss the problems associated with regulating the synthesis of pheromones and with transporting such insoluble compounds through the body and delivering them to their target tissues. The symposium concludes with a discussion of cuticular pheromones in insects and their roles in colony- and mate-recognition (Singer).

Two themes emerge in the course of this symposium. The first is the interconnections between seemingly disparate areas of lipid biology. For example, regulation of membrane saturation is central to homeoviscous adaptation in the face of varying temperature. However, unsaturated fatty acids also are the precursors for biosynthesis of prostaglandins and eicosanoids. Similarly, cholesterol affects membrane fluidity, and is a precursor for a wide range of steroid hormones. The common biosynthetic pathways of lipids link their functions in ways that remain poorly understood.

The second major theme is the multifunctionality of lipids. A prime example comes from the surface lipids of terrestrial animals. In arthropods, the same hydrocarbons used in chemical communication may be major components of the cuticular waterproofing barrier. In mammals, cholesterol and other sterols play a similar role in the stratum corneum (Downing, 1976). The interactions between different functions of the same lipid compounds are only now beginning to be addressed. We predict that future physiological and evolutionary studies of lipid biology will eventually provide a truly integrative understanding of lipids.

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