Book Reviews

Modes of Restoring Diploidy

Biology of Fertilization. CHARLES B. METZ and ALBERTO MONROY, Eds. Academic Press, Orlando, FL, 1985. In three volumes. Vol. 1, Model Systems and Oogenesis. xviii, 391 pp., illus. $75. Vol. 2, Biology of the Sperm. xx, 475 pp., illus. $75. Vol. 3, The Fertilization Response of the Egg. xviii, 469 pp., illus. $75.

Fertilization occurs but once in the life history of the organism, but the changes associated with fertilization are not once-in-a-lifetime events. Rather, the few seconds around sperm-egg contact represent a microcosm of cell biological phenomena, including cell-cell recognition, cell attachment, cell fusion, signal transduction involving polyphosphoinositides, calcium, and *p*H increases, exocytosis, endocytosis, changes in actin and tubulin, a large augmentation of protein synthesis, and, finally, initiation of DNA synthesis, which ultimately culminates in a series of rapid mitotic divisions.

Overlying the vast number of cellular and chemical changes, the morphological aspects of fertilization seem boringly similar among different species—a small motile sperm fuses with a large nonmotile egg, and this interaction somehow triggers development. Yet one comes away from reading this three-volume collection awed by the different mechanisms used to achieve the same end.

A good example of the similarities and differences is seen in the mechanisms by which oocytes of different organisms complete the meiotic divisions. The oocyte remains in meiosis until just prior to ovulation; the completion of meiosis and the formation of the haploid cell is then typically triggered by a hormonal system. In the best-studied cases—oocytes of starfish and frogs—a neuropeptide acts on the ovarian cells to produce a substance that has a low molecular weight, and this then acts at the cell surface to induce completion of meiosis and associated changes that allow the egg to be fertilized. As reviewed in excellent papers by Kanatani and Masui, the principles used are similar but the actors are radically different. The dissimilar actors are the hormones—the starfish uses a nucleoside derivative and the frog a steroid. The similarity is that in all cases the cascade of events ensuing from the interaction of hormone and plasma membrane results in the formation of similar cytoplasmic proteins that then induce meiosis. The same principle is apparently used in all cells for meiosis or mitosis—one can extract protein factors from dividing somatic cells that may be identical to the factors produced in oocytes and that act by causing a breakdown of nuclear membranes and the condensation of chromosomes.

An even more striking example of how the same ends are achieved by different means is seen in an elegant review by Tilney on the acrosome reaction and the formation of the acrosomal process. The acrosomal process is an extension of the cell, forming at the apical end of the sperm upon contact with the egg jelly. In echinoderm sperm, the formation of the acrosomal process involves an explosive polymerization of actin. In horseshoe crab sperm, actin filaments are already preformed and the extension of the acrosomal process occurs via changes in the twist or pitch of the coiled actin filaments. Here then different mechanisms achieve the identical morphological outcome.

A final example is an apparent molecular coevolution in the mechanisms by which the sperm approximates contact with the egg surface preparatory to fusion. Eggs are typically surrounded by an envelope (the chorion), and sperm possess mechanisms to pass through this envelope to get to the egg surface. Hoshi reviews these rites of passage and notes that in most cases the entry is via activity of hydrolytic enzymes associated with the sperm. In some cases, however, a nonenzymatic mechanism is used in which sperm-associated proteins somehow destabilize the egg envelope so that a hole is made through which the sperm can pass. No hydrolases are involved. Clearly, reciprocal evolutionary changes in both sperm and egg components must have occurred in order for this novel mechanism to be used.

To be sure, there are similarities in how embryonic development is initiated. It appears that in all cases activation ensues from receptor-mediated increases in cytosolic calcium in the egg. But even here there may be phyletic variations. Jaffe notes that calcium is released from cytoplasmic stores in some types of eggs, whereas in others the Ca^{2+} increase comes from influx into the egg.

The evolutionary caprices surrounding fertilization, which I have chosen to emphasize in this review, are really not surprising. The developmental stages centering on formation of the gametes and their fertilization are really the arena where evolutionary variation occurs. The ability to move to different environments, for example from aquatic to terrestrial, depended on evolving new types of egg coats. Meiosis is synonymous with crossing-over, gene recombination, and the opportunity for gene duplications in the germline. Fertilization involves species-specific reciprocal receptors for gamete binding, and changes in these receptors would favor reproductive isolation and subsequent speciation.

Many of the phenomena associated with early development are covered in these three volumes. There are chapters on egg and sperm formation, egg and sperm maturation, adhesion, recognition, and chemotaxis in prokaryotes and eukaryotes as well as important papers on the aforementioned cell biological phenomena. There are also chapters on embryological concomitants of fertilization, such as a paper by Malacinski on fertilization and axis formation in amphibian embryos and important reviews from the labs of Davidson and Raff on the macromolecular correlates of early embryogenesis.

This series provides a good review of fertilization, circa 1986, and is published almost 20 years after the first similar treatise. I suspect that the next update will be needed much sooner and that at that time an even better understanding and appreciation of the similar, yet so varied, modes of restoring diploidy will be available.

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Apis mellifera

Honeybee Ecology. A Study of Adaptation in Social Life. THOMAS D. SEELEY. Princeton University Press, Princeton, NJ, 1985. x, 202 pp., illus. $39.50; paper, $14.50. Monographs in Behavior and Ecology.

In science as in history the honeybee *Apis mellifera* has reigned as our premier social insect. William Morton Wheeler observed that in antiquity its great industry and many useful products, of mysterious origin, made the honeybee "a divine being, a prime favorite of the gods, that had somehow survived the golden age or had voluntarily escaped from the garden of Eden with poor fallen man for the purpose of sweetening his bitter lot." In more recent times it has become one of the most intensively studied of all animal species, especially with reference to behavior and social organization.

Research on the honeybee in this century can be divided into two principal periods. The first, led by Karl von Frisch from 1914 into the 1950's, stressed physiology and ethology. A great deal was learned about what honeybees do: the basic properties of their sensory perception, division of labor, colony life cycle, aging, communication by pheromones, the now-famous waggle dance, and other aspects, enough to fill tens of thousands of articles in over 20 journals devoted entirely to the species. During the

1950's the second period began under the leadership of von Frisch's student Martin Lindauer and a few others. Close attention was paid for the first time to the other species of *Apis*, which occur in southern Asia, and the independently evolved stingless bees of the Old and New World tropics. A more evolutionary interpretation was attempted of the adaptive functions of the distinctive traits of *Apis mellifera*, now viewed as but one species whose history had been played out under environmental circumstances peculiar to the Old World tropics and warm temperate zones.

The latter approach, which augmented but in no way supplanted the older mode of research, gained new impetus during the 1970's when field and experimental research came under the influence of the relatively new disciplines of behavioral ecology and sociobiology. Among the leaders of this latest advance has been Thomas D. Seeley of Yale University (perhaps best known to the non-entomological public as the developer with Matthew S. Meselson of the bee-feces hypothesis of yellow rain). Seeley's research has been notable in combining experimental designs marked by flair and originality reminiscent of the von Frisch school with theoretical questions based on a sophisticated reading of natural selection theory. *Honeybee Ecology* is a terse and well-written book that summarizes his own and related research. It is a worthy successor to Lindauer's *Communication among Social Bees* (1961) and C. D. Michener's treatment of *Apis* in *The Social Behavior of the Bees: A Comparative Study* (1974), a masterly statement of what we know about honeybee behavior and, equally important, of why honeybees behave in such and such a way and not another.

A couple of examples from Seeley's research will convey the overall flavor of current research on honeybees, as well as the study of social insects more generally. The first is from the domain of behavioral ecology. P. K. Visscher and Seeley monitored the foraging activity of a colony by translating the workers' own waggle dance, which gives information on the direction and distance of the flower beds being visited. The method was augmented by recording the different species of pollen brought in by the bees. The data were plotted onto circular maps with the hive in the center, so that the destinations of the foragers could be followed as though they were moving objects on a radar screen. The results included some surprises, including the fact that a single colony patrols an area of over 100 square kilometers and brings in food from an average distance of 2000 meters. Workers occasionally work over 6 kilometers away, although the most common patch distance was 600 to 800 meters. If we translate this into human terms, the activity is the equivalent of a tribe of 30,000 or so people hunting for food in a circular area with a radius of about 800 kilometers—say the whole state of Texas out of Abilene. The bees' exquisite communication system allows them to shift the focus of their activity on a day-to-day basis across the immense terrain, a pattern that Seeley calls the "information-center strategy" of foraging.

The second example is from the related field of sociobiology. A fruitful debate among students of social insects has been whether the insect colony is a concoction of the queen who forces her offspring into raising their brothers and sisters instead of their own offspring or whether it arose because the workers find it more profitable to rear siblings in a social setting than offspring in solitude. Seeley shows that honeybee workers do not start laying eggs on their own until both the queen and the brood are absent. In other words, only when the workers have lost all chance of rearing a substitute queen do they resort to direct reproduction of their own. Furthermore, workers are inhibited from rearing new queens by a special "queen substance," 9-ketodecenoic acid, which the old queen manufactures in her oversized mandibular glands. But the inhibitory material is not forced on the workers by their mother. Quite the opposite: workers visit the queen to collect the substance, then travel through the hive to share it with their nestmates. The whole procedure appears to be a method of monitoring the presence or absence of the queen on a day-to-day basis. Seeley concludes that "the present-day social system of honeybee colonies is evidently not one of a despotic queen ceaselessly dominating the reproduction of thousands of worker-daughters, but rather one of workers themselves benefiting by providing for the well-being of their queen, the individual whose reproduction provides their best avenue for propagating their genes."

Because nervous systems are evolutionary products subject as much to the idiosyncrasies of long-term history as to principles of molecular genetics, behavioral biology must progress in good part by the comparison of carefully chosen paradigm species. Seeley's book takes its place among such recent works as Daniel E. Koshland's *Bacterial Chemotaxis as a Model Behavioral System* and Eric R. Kandel's *Cellular Basis of Behavior* (featuring the marine snail *Aplysia*) as a fine exemplar of this approach.

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Plant History

Geological Factors and the Evolution of Plants. BRUCE H. TIFFNEY, Ed. Yale University Press, New Haven, CT, 1985. viii, 294 pp., illus. $25. From a symposium, Montreal, 1982.

This book contains a collection of papers presented at the Third North American Paleontological Convention. In the words of the editor, the intention was to discuss "the synergistic interaction of organisms and environment as viewed on the paleontological time scale." Such an all-embracing assignment is bound to be inadequately carried out in a volume of just under 300 pages. Nevertheless this is, on the whole, a readable, informative, and stimulating book.

An introductory chapter by Tiffney puts the papers in an evolutionary context and raises a series of fundamental questions regarding synergistic interactions of the past. Unfortunately, some of his questions (for example those relating to the Mesozoic) are left unaddressed because the papers that follow are strongly biased toward the Paleozoic.

Following examinations of the origin of autotrophic eukaryotes (by Awramik and Valentine) and biochemical aspects of the origin of land plants (Chapman) Beerbower paints a vivid picture of the harsh terrestrial environment prior to and during the invasion by plants.

Three papers deal with the reconstruction of global paleogeography, paleoclimate, and phytogeography. Barrett's paper outlining early Devonian paleogeography and climate appears to have been a casualty of the three years "in press." His techniques are similar to those published previously by Parrish, and many of the points he raises are reiterated in this volume by Raymond, Parker, and Barrett ("Early Devonian phytogeography") and Raymond, Parker, and Parrish ("Phytogeography and paleoclimate of the early Carboniferous"). In fact the repetition, though it allows the papers to stand alone, is tedious for anyone reading the volume as a whole, but the authors of both phytogeographic papers are to be commended for stating clearly the criteria for data inclusion and for taking into account possible sources of bias such as taxonomic and depositional sorting factors. It is to be hoped that these papers will set a standard for subsequent work of this type. However, the paper on Devonian phytogeography is not without flaws. Early Devonian land plants characteristically had simple yet rapidly evolving morphologies and were capable (through homospory) of long-distance dispersal. Under these circumstances only the narrowest of time slices are likely to yield meaningful