Book Reviews


Both books address the role developmental biology plays (or should play) in the study of evolution. One can hardly imagine two books on a similar subject that are more different than these two. They differ almost completely in their content, style, and density of information. In fact, neither book cites any work of author(s) of the other book.

The book by John and Miklos is a fairly extensive review of a number of subjects in the general areas of genome organization, developmental biology, and molecular evolution. Its nearly 50 pages of references make it a useful introduction to many of the subjects treated. The topics range from yeast mating type and immunoglobulin class switch, to *Drosophila* neural genetics, sex determination, and dosage compensation, to interspecific cytogenetic comparisons and molecular drive. The main emphasis is the molecular and developmental mechanisms of evolution. Since it covers such a large territory, we expect some errors and exasperating statements, and they are not infrequent. It takes a few readings to skip such irritating points and see the large picture the authors try to portray. Of course, it would be quite an accomplishment to tie all the subjects together. The authors fall somewhat short of it, as the book reads like two books in one: chapters 1, 3, and 4 on genome organization/molecular evolution and chapters 2 and 5 on development. Nevertheless, it is still a very informative and readable book.

The review on comparative genome organization and coding capacities is thorough. The authors' general strategy of presenting *Drosophila* studies in great detail, followed by a more comprehensive discussion of other organisms, seems to pay off well. In these chapters, John and Miklos stress a common theme—i.e., that much of eukaryotic genomes consists of redundant (junk) DNAs—by providing a good glimpse of the capriciousness of some aspects of genome organization, e.g., the widely varying abundance of heterochromatic satellite DNAs between closely related species. However, direct functional assays that are needed to prove their claim (that the presence or absence of heterochromatic satellite DNAs has no effect on the fitnesses of individuals) are not as convincing as they want us to believe. Most of all, they do not present a single case where homozygotes for a deletion of satellite DNA are as fit as the original chromosome. Genetic manipulations cited are either *adding* a mini-X fragment (which is not the same as deleting something) or deleting heterochromatic materials together with the neighboring essential genes, such as rDNA. Furthermore, the assays are not on fitness differences but are on various attributes, such as chromosome pairing, hatching time, or transcription.

In their earnest attempt to convince the readers of the junk-DNA notion, John and Miklos do not explore in depth the possibility that satellite DNAs may play a role entirely different from that of euchromatic genes. For instance, they may simply be a structural component of chromosomes. Recent progress on heterochromatic phenomena offers some interesting insight. For example, chromosome condensation is relaxed if bending of satellite DNA in the centromeric heterochromatin is altered (Radic et al. 1987). Segregation distorer in *Drosophila,* a system that one of the authors studied

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previously, involves heterochromatic satellite DNA that appears to affect chromatin condensation, transmission distortion, and chromosome evolution. For all we know, the function of heterochromatin may be compared to the speeches of 2-year-olds—both are unstructured, variable, imprecise, and nearly unanalyzable, but both may still serve a useful purpose for those possessing them.

While stressing the importance of the molecular/developmental mechanisms of morphological evolution, the authors at times seem to imply that evolutionary biology is no more and no less than those mechanisms. This view leads to an uneven and sometimes unrigorous treatment of topics. Molecular drive is enthusiastically discussed because "the internal genomic readjustments generated by molecular drive (may) have played a role in generating evolutionary novelty." The next sentence is: "The dilemma is that we have scant data for the molecular basis of any form of morphological change" (p. 243). On the other hand, other evolutionary topics (including molecular evolution) are discussed almost casually. Fitness is defined in biochemical/cytological terms. For example, the formation of interspecific dimers is taken as evidence that the amino acid substitutions are neutral, while a normal appearance of chromosome pairing or a normal hatching time is said to be evidence for a lack of a fitness effect. Punctualism is lumped together with the neutral theory in a very small section under the heading of neutral drift. Overall, the authors contend that molecular developmental biology holds the key to many (most?) difficult questions in evolutionary biology. Where I disagree with them is in the role of classical studies in this new era. A case in point is their prescription for studying reproductive isolation. They emphasize, almost exclusively, molecular events such as molecular drive in multigene families. I believe old-fashioned genetics (by Dobzhansky, Muller, Pontecorvo, and newcomers) coupled with new molecular techniques, such as RFLP mapping and protein 2D gels, is the way to go.

While one may agree or disagree with John and Miklos, their book is at least informative about recent exciting progresses. I wish I could say the same thing about Arthur's book. The morphogenetic tree theory is a useful way to visualize some aspects of development, and it generalizes developmental changes that are important in evolution. However, I am not sure how such an abstraction can help us in elucidating the mechanisms of development and evolution.

For an evolutionary geneticist trying to make sense out of recent excitement in developmental biology, Arthur's book is not going to help much. Perhaps it was not his intention to incorporate these new studies. Still, I find it hard to believe that a new book on development cites almost no developmental biology papers later than 1980. The exceptions are those about homeoboxes. It is also inconceivable that he completely ignores the Raff and Kaufman (1983) book on a very similar subject.

LITERATURE CITED


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For the past decade, Doug Futuyma's *Evolutionary Biology* has been the standard advanced undergraduate/graduate text on evolution. Avers's *Process and Pattern in Evolution* is the newest competitor, although it is a somewhat more introductory-level text. Avers fundamentally departs from Futuyma in that her text is largely written from a cell-biology perspective. This is both the major strength and the weakness of her book. The reader is exposed to a molecular biology–biased view of evolution, providing a contrast to the organism-biased view presented by Futuyma. For this reason, this is the wrong evolution text for a reader with a molecular background. For example, the text has no mention of the genetics of complex characters, reinforcing the current trend in molecular evolution to treat evolution as a series of single-locus problems. The book mirrors much of molecular evolution in being critical when examining evolutionary patterns but uncritical when examining evolutionary process.

*Process and Pattern* is divided into three main sections: “Foundations of Life on Earth,” “Evolutionary Processes,” and “Patterns and Trends in Evolution.” “Foundations” gives a highly readable and fairly complete review of current theories on the origin of life, and it consists of chapters on the origin of evolutionary ideas, the physical/chemical settings for life, the origin and evolution of primeval life, and an overview of the major evolutionary themes in cell biology. The chapters on these last three topics amount to a compressed cross between Day's *Genesis on Planet Earth* and Loomis's *Four Billion Years* and make interesting reading. While Avers gives an extensive discussion of self-splicing group I introns as models for the earliest replicators, there is no mention of self-splicing in plant satellite RNA and viroids. Self-splicing is a critical step in the replication of these RNAs, providing perhaps a more realistic model for early replicators, especially in light of the recent characterization of the "hammerhead" motif required for splicing (Forster and Symons 1987).

The discussion on the nature and importance of introns has problems. First, no mention is made of the very distinct classes of introns (groups I and II, nuclear Pol II, and nuclear tRNA); rather, the term “intron” is used for all. Second, the contention that introns were likely present in the first prokaryotes is an uncritical review, with the opposite view—that introns were fairly recently (e.g., around 1 billion years ago) introduced—not being presented. The two main pieces of evidence for an early origin of Pol II introns are that (1) intron positions in some genes shared by both prokaryotes and eukaryotes are partly conserved in eukaryotes as divergent as *Aspergillus*, maize, and vertebrates and (2) exon positions for genes shared by both prokaryotes and eukaryotes appear to correspond with protein domains. Observation (1) tells us only that introns were present fairly early in the main branch of the eukaryotic lineage, although there are a number of interesting eukaryotes that branch considerably deeper than does the *Aspergillus/maize/vertebrate* most recent common ancestor (e.g., see Vossbrinck et al. 1987). The proposed correlation between exons and protein domains in ancient genes shared by prokaryotes and eukaryotes has not been subjected to any statistical analysis. Rather, the interpretation has been very subjective. The null hypothesis—that the observed exon-domain correlation is random—has not been tested. One could construct the expected correlation under the null hypothesis by randomly placing intron (constrained by the known size distribution of exons) into the cDNA sequence of the protein in question and examining the nature of correlations between exons and domains in these artificial sequences, but this has not been done.

Avers states that the “role of introns” is in constructing new genes, strongly implying that introns evolved because they construct genes, rather than that the presence of introns facilitates exon shuffling. Three distinct issues are confused by such statements: the evolutionary origin of introns, the maintenance of introns, and the consequences of having introns. This sort of confusion between the consequences of a particular genetic structure and the evolutionary mechanisms for the origin and/or maintenance of that structure is rampant in the molecular evolution literature, and
it is especially troublesome that it has found its way into an introductory text. A similar example is Avers's statement that "other repetitive DNA appears to be essential for survival. For example, tens of millions of copies of genetically inert, short sequences surround the centromere." However, population genetic models indicate that long tandem arrays tend to accumulate in regions of low recombination (such as near a centromere), which provides an explanation for the localization of such sequences without them being essential.

The "Foundations" section concludes with discussions on various endosymbiotic theories and on the major evolutionary lineages. Avers leaves the reader with the feeling that Margulis's notion of eukaryotic flagella having an endosymbiotic origin has as much support as does an endosymbiotic origin of mitochondria. The discussion of major evolutionary lineages presents both the Whittaker-Margulis five-kingdoms scheme and the Woese scheme of three major deep lineages (i.e., archaeabacteria, eu-bacteria, and eukaryotes). The five-kingdom scheme was important in that it emphasized the diversity in the lower eukaryotes, but I find it very troublesome in that it (1) groups the tremendous bacterial diversity into a single kingdom; (2) gives the false impression that plants, fungi, and animals are fairly phylogenetically "deep" relative to the rest of the eukaryotes (when, in fact, they are near the upper branches of the eukaryotic lineage; see Vossbrinck et al. 1987); and (3) has a branching order that appears to be somewhat arbitrary, rather than being inferred by phylogenetic reconstruction methods.

The four chapters constituting the section on "Evolutionary Processes" cover standard micro- and macroevolution and are, by far, the weakest part of the book. For example, Avers applies terms for selection on phenotypes to situations of selection on a single locus. Purifying selection (selection to remove most new mutations at a given locus) is called "stabilizing selection," while the figure (6.7) discussing stabilizing selection on phenotypes shows no decrease in phenotypic variance due to selection. Disruptive selection is defined as selection acting against less fit heterozygotes, rather than as selection acting against intermediate phenotypes. Kimura's neutral theory is defined as "the virtual absence of selective forces at the molecular level," when in many cases it requires, in fact, strong purifying selection. The Drosophila ADH polymorphism is discussed, but the critical work, by Kreitman (1983) and others, on the molecular characterization of these variants is not mentioned. Avers states that "the frequencies of lethal alleles are very low, but they persist because selection is relatively ineffective when frequencies are rare." Mutation/selection balance as an explanation is not mentioned for this case. Another statement is that mutation is regarded as a relatively weak force in evolution. This is correct in terms of changing gene frequencies, but mutation is by no means trivial in terms of introducing variation. Other important references missed are the recent work by Coyne and Orr on the genetics of reproductive isolation in Drosophila and Gillespie's work on variation in the molecular clock.

The final section, "Patterns and Trends," gives a reasonable overview of methods for reconstructing phylogenies (giving a balanced presentation of cladistics and phe-netics) and concludes with an extensive review of primate and hominine evolution. In summary, Process and Pattern provides a useful introduction to the pattern of evolution but does little to elucidate the process. For the average Molecular Biology and Evolution reader, who has a molecular background and is trying to hone his or her evolutionary skills, this is the wrong book, as it tends to reinforce bad habits in thinking about evolution. It is, however, a nice introduction to evolutionary patterns.

LITERATURE CITED


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