BOOK REVIEWS

Evolutionary Revelations

Molecular Markers, Natural History and Evolution. JOHN C. AVISE. Chapman & Hall, New York, 1994. xiv, 511 pp., illus. $89.95 or £75; paper, $37.50 or £24.99.

Perhaps the most widespread misconception about molecular evolutionary studies is that they represent reductionistic attempts to explain evolution in terms of genic-level properties and causes. The molecular evolutionist is often caricatured running gels and collecting DNA sequences to the detriment of knowledge of organismal biology, behavior, population biology, and ecology. *Molecular Markers, Natural History and Evolution* shows how erroneous this perception is. Molecular markers have revealed many dimensions of organismal and populational biology that formerly were inaccessible for most natural populations: systems of mating, kinship and kin recognition, population structures and gene flow, philopatry, dynamics of hybrid zones, geographic distributions of clonal organisms, geographical and genetic boundaries of biological species, interspecific phylogenetic relationships, and historical biogeography. The genetic structures of populations and phylogenetic relationships among species provide the historical frameworks within which studies of microevolutionary and macroevolutionary phenomena are unified and synthesized. The focus of Avise's book is not molecular evolution *per se* but the evolutionary patterns and processes revealed at all levels of biological complexity by molecular markers.

Avise shows how molecular studies have revolutionized population genetics over the past several decades. Beginning in the 1960s, electrophoretic studies of protein variation permitted for the first time routine measurements of allelic frequency variation within and among populations. These studies revealed extensive genetic variation and generated the controversy regarding selective importance versus neutrality of genetic polymorphisms, a debate that has dominated population genetics for the past 25 years. While acknowledging the historical importance of this debate, Avise sees no definitive resolution forthcoming and suggests that the most productive directions for population genetic research lie elsewhere, in phylogenetic studies of DNA sequences. Population genetics gains a powerful historical dimension when phylogenetic relationships among the different allelic forms of genes are studied in addition to their frequencies in populations. Avise applies the term "phylogeography" to the study of the principles and processes governing geographical distributions of genealogical lineages both within and between species. Much of the book is devoted to showing how phylogeographic studies of the maternally transmitted mitochondrial DNA of animals provide insights into historical processes of gene flow, speciation, and hybridization among natural populations. The mathematical foundations of population genetics likewise have become explicitly historical through recent developments in coalescent theory.

Molecular phylogenetics forms a conceptual bridge between the formerly largely separate disciplines of population genetics (microevolution) and traditional phylogenetics (macroevolution). Avise illustrates diverse molecular approaches to studying interspecific phylogenetic relationships while cautioning that molecular phylogenies do not necessarily recover the phylogenies of the populational lineages in which they are found. Two particularly strong claims are made for molecular studies of interspecific phylogeny: (i) that molecular data can distinguish homology from analogy and (ii) that molecular data provide "common yardsticks" for measuring evolutionary divergence among disparate lineages. Molecular data have set rigorous standards for testing phylogenetic hypotheses, and I suspect that strictly nonmolecular phylogenetic studies of most extant taxa ultimately will fall short of these standards. Molecular phylogenetic characters may be most effective, however, when analyzed together with morphological and behavioral characters, an issue that Avise does not address. Phylogenetic signal can be enhanced relative to "noise" when characters representing different levels of biological complexity are analyzed together. Molecular data alone are unlikely ever to resolve short, internal branches located deep in the phylogenetic history of a group. Such branches can be revealed by morphological characters that arose on them and subsequently became burdened by functional or developmental constraints imparting evolutionary stability. Such characters may be crucial for studying rapid adaptive radiations that occurred in the distant evolutionary past.

Avise reviews numerous empirical studies representing nearly all of the molecular population genetic and phylogenetic approaches explored throughout the past three decades. Technical descriptions of the molecular techniques and analytical methods make this work highly accessible. A chapter on conservation genetics illustrates numerous practical applications of this knowledge. Avise's coverage is largely nonmathematical, and the treatment complements earlier books on molecular population genetics and evolution that generally have placed great emphasis on mathematical theory.

Molecular phylogenetics, together with recent developments in evolutionary paleontology, have given evolutionary biology a synthetic historical and hierarchical perspective that constitutes what may be the most important advancement of Darwinian evolutionary theory achieved during this century. Phylogenetic approaches to the study of adaptation, speciation, and community structure are replacing the more limited approaches used prior to the general availability of knowledge of phylogenetic history. Avise's book is a timely synthesis of

Prices of Books

Average per-volume prices of books reviewed in *Science* 1989–1994. The average prices per page for the technical books in the natural sciences for the years covered were 16.9¢, 17.8¢, 17.0¢, 17.2¢, 17.2¢, and 18.3¢. (Data are for hard-cover books except where books were available only in paperback.) For earlier data from *Science* and other relevant information see *Science* **211**, 933 (1981); **235**, 95 (1986); **239**, 81 (1987); **243**, 99 (1989).

Category	Price (dollars)					
	1989	1990	1991	1992	1993	1994
All books	54.58	54.43	54.08	57.58	51.21	59.96
Technical books in natural sciences	73.73	75.57	73.19	76.78	79.00	81.93

the molecular phylogenetic discoveries on which the future of evolutionary biology will be built.

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Solid Flows

Granular Matter. An Interdisciplinary Approach. ANITA MEHTA, Ed. Springer-Verlag, New York, 1994. xii, 306 pp., illus. $89 or DM 158.

Disorder and Granular Media. D. BIDEAU and A. HANSEN, Eds. North-Holland (Elsevier), New York, 1993. xxiv, 323 pp., illus. Paper, $80. Random Materials and Processes.

Practically everyone is aware that salt, pepper, soil, sand, a collection of marbles, and many other materials composed of discrete solid particles can be made to flow in a way that is reminiscent of the flow of fluids. The abundance of such media, also known as granular materials, and the economic importance of coal, cereals, pills, and other granular materials are undeniable, and the dynamics of solid pollutants is of environmental concern. Collections of solid particles cannot always be considered as granular materials but should be referred to as suspensions when the ambient fluid is of dynamical importance.

Naturally, a rich engineering literature is devoted to the statics and dynamics of this class of materials. The increased use of coal as an energy source in power plants and the need to develop reliable models for its behavior in static and fluidized cases have significantly encouraged research in this area. Though the study of granular matter is not limited to "applied" science—astrophysicists have studied the dynamics of interstellar dust and rocks (in part in order to understand some properties of Saturn's rings)—the physics community on the whole had not devoted much attention to the interesting and unique phenomena characterizing these materials prior to the work on the effect of "self-organized criticality" by Bak, Tang, and Wiesenfeld. As Mehta discusses in the opening chapter of *Granular Matter*, this work, while presenting a highly oversimplified model of a sandpile (the demonstration Bak *et al.* used), has attracted the attention of physicists to granular materials. It is rather curious that some physicists were interested in this field a long time ago: work on the stability of piles composed of granular materials, such as sandpiles, dates back to Coulomb (the very same Coulomb who was responsible for the formulation of the law of electrostatic interactions) in 1776, and the idea of dilatancy, that is, that a granular medium must dilate as it is set into motion, was published by Hagen in 1852 and by Reynolds in 1885.

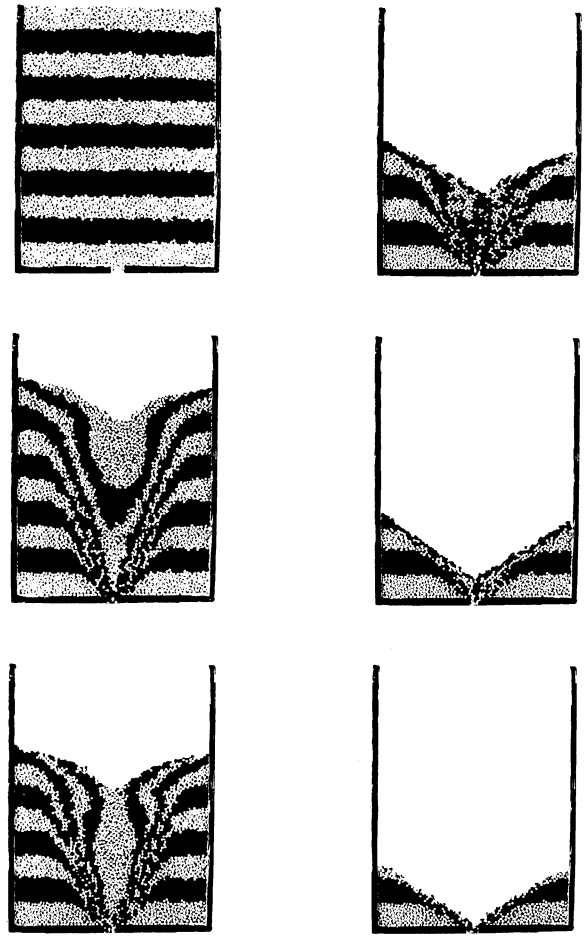
Newcomers to the field of granular materials have not been able to find basic textbooks on the subject, and even review articles on the statics or dynamics of granular matter were next to nonexistent up to a few years ago. The appearance of two new books on granular materials is thus very welcome. Neither is a textbook, but both are written for nonspecialists (particularly physicists). They can be useful to specialists as well, since they cover a larger variety of topics than can be in the area of specialization of a single person. Some related subjects, such as suspensions and colloidal suspensions, are reviewed in them as well. The editors of both books have clearly attempted to achieve a balance among theory, experiment, and simulations.

Bideau and Hansen's *Disorder and Granular Media* seems to cater more to the interests of physicists and applied mathematicians in presenting an extended exposition of the properties of disk and sphere (two- and three-dimensional) packings. This information is of course useful to applied physicists or engineers, but it is not central to their interests. Other papers in the book describe deposition models and the dynamics of porous media as well as the dynamics of dense suspensions, all of which are closely related to granular materials and thus topics with which researchers in the field need to be familiar. The engineer will find in this book a clear exposition and applications of some important concepts and theories, such as scaling and percolation theory, which have been thoroughly studied by physicists and applied mathematicians. The physicist will find in this book some good introductory expositions of topics in the field.

Granular Matter, in addition to the contribution by the editor in which the nature of "real sandpiles" is explained and contrasted with the toy sandpiles that some physicists have been playing with, includes an interesting attempt by Edwards to define a thermodynamic theory of powders. Papers characterizing the mixing and segregation of granular materials as well as expositions of continuum mechanical and micromechanical descriptions make contact with important applications, while providing good introductions to the subject.

One of the important topics that is not covered in either book (though it is referenced in both) is that of rapid granular flows and the kinetic theoretical approach to this problem. This subfield has been of much interest to engineers and of less to physicists.

The presentation in both books is very clear, and the extensive (and up-to-date) lists of references are very useful. Both books make it perfectly clear that granular materials exhibit a large number of interesting and unusual rheological properties, that the physics of these materials is unique and challenging, that many of their features are poorly understood, and that the range of applicability of the concept of a granular material is very wide indeed. Some of the modern experimental techniques and numerical methods that are presented in the books should be of interest to both specialists and nonspecialists.



"Emptying of nearly spherical particles from a rectangular two-dimensional hopper." [From S. B. Savage's paper in *Disorder and Granular Media*]