The book is massive, weighing a hefty 2.6 kilograms, but is a bargain in today's world of inflated prices. Stanford University Press has given it its due; it is well designed and the typography is exceptionally clear.

Interestingly, the volume was published in the same year as two other well-illustrated floras covering small areas in the American tropics: C. H. Dodson and A. H. Gentry's "Flora of the Rio Palenque Science Center, Los Rios, Ecuador," *Selbyana* **4**, 1-628 (1978), and J. A. Steyermark and O. Huber's *Flora del Avila* (Ministerio del Ambiente y de los Recursos Naturales Renovables, Caracas, Venezuela, 1978). Together, these works can serve as stepping-stones into the world's richest floristic region while more comprehensive, large-scale floras are being prepared.

Recent international agreements and increased use by Panamanian students make one hopeful that Barro Colorado Island will continue to support research for decades to come. With Croat's impressive flora to add to the host of earlier work, current and future researchers should find this little island especially hospitable for more refined and intensive work in a very diverse tropical forest ecosystem.

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Heterogeneity and Evolution

Marine Organisms. Genetics, Ecology, and Evolution. Proceedings of a conference, Venice, March 1977. BRUNO BATTAGLIA and JOHN A. BEARDMORE, Eds. Plenum, New York, 1978. x, 758 pp., illus. $49.50. NATO Conference Series IV, vol. 2.

Assuming the central dogma of molecular biology (DNA→RNA→protein) and utilizing the methods of protein electrophoresis, geneticists in 1966 identified for the first time not only polymorphic but also monomorphic loci. This identification made possible the estimation of genetic variability. Although exceptions have been reported, the initial estimates of approximately 5 to 15 percent heterozygosity calculated for humans and flies have proved to be generally predictive of the vast amount of variability present in most populations. The discovery of this store of electrophoretically detectable variability sparked the neutralist-selectionist debate over the biological significance of this allozymic variation. The selectionist school argued that the allozyme variants were balanced polymorphisms maintained by natural selection. Neutralists, on the other hand, explained the same data sets by arguing that selection was unable to perceive the differences between most allozymes and that they were present in natural populations owing to the interplay of recurrent mutation and effective population size. Most of the allozyme studies or surveys published in the years just following the initial reports attempted to resolve the controversy by showing generalized agreement or disagreement with predictions of the neutral model. The accuracy of mutation and population size parameter estimates was not such as to permit resolution of the debate, and apparent victories were quickly and predictably nullified by counterarguments or interpretations. Fortunately the heat of the debate attracted a great deal of attention, and many of those attracted brought with them old questions to which the techniques of gel electrophoresis could be applied. This has increased intellectual cross-fertilization among geneticists, ecologists, taxonomists, physiologists, and developmental biologists. The techniques were soon employed in studies of spatial and temporal patterns of variability and in quantifying genetic divergence between different taxonomic levels. Electrophoretic identification of protein variants was, quite clearly, a technique of great utility for ecology and evolutionary systematics as well as for genetics. It not only permitted identification of monomorphic loci, it allowed quasi-genetic study of organisms that could not be cultured in the laboratory.

By 1970 a number of marine biologists had begun electrophoretic studies and others had begun to apply these techniques to marine organisms. This book contains the proceedings of a NATO Advanced Research Institute organized to bring together a sample of those working on the genetics, ecology, and evolution of marine organisms. The majority of the 33 papers deal, in one way or another, with electrophoretic studies; the remaining papers provide interesting parallel approaches to questions addressed electrophoretically by other contributors. The papers are grouped into five sections: measurement and maintenance of genetic variation, ecology and life history, taxonomy, sex determination and breeding systems, and applied genetics. The grouping is somewhat arbitrary, and the reader interested in only one topic will have to use the index to guide the section-jumping necessary to obtain an appreciation of the cross-fertilization of ideas and questions contained in the volume.

One topic addressed by many of the contributors is the rather obvious, if somewhat difficult to delineate, prediction of ecological genetics that genetic variability should be related to physical or biotic environmental heterogeneity. Assuming that allozyme variation is subject to natural selection, estimation of genetic variability in organisms occupying different environments permits testing of these correlational hypotheses. A variety of hypotheses have been proposed in an attempt to predict correlation of environmental and genetic heterogeneity. One, proposed by Bretsky and Lorenz in 1969, was that extinction patterns in the fossil record could be explained on the basis of a positive correlation between genetic variability and environmental stability. That is, organisms in stable environments are expected to have less variable gene pools, owing to specialized adaptation; as a consequence they are unable to adapt to major environmental changes, and extinction rates are expected to be higher for such organisms. Studies of the giant clam *Tridacna maxima* and deep-sea asteroids by Ayala, Valentine, and Hedgecock uncovered unexpectedly high amounts of genetic variability. Since these organisms had been selected for study because they lived in stable environments, an explanation of their high variability was required. According to the trophic-resource-stability hypothesis of Ayala and Valentine, organisms in temporally stable environments are able to perceive their spatial environment as coarse-grained. The luxury of trophic stability permits them to adapt genetically to the coarse grain. Ayala and Valentine's evidence, discussed by them in two contributions, is consistent with this hypothesis. The estimates Ward and Galleguillos present of average heterozygosity in three temperate-zone teleosts are at variance with the prediction of the trophic-resource-stability hypothesis if class averages for heterozygosity estimates are admissible. Fish exhibit heterozygosities in the vertebrate range of approximately 0.05; plaice, dab, and flounder, studied by Ward and Galleguillos, exceed this value. Greater heterozygosity is not expected, because the trophic-resource stability for these three species is expected to be low. Like the earlier clam and asteroid studies, however, this study is merely suggestive. The level of abstraction is very high, and, as Ayala and Valentine point out, trophic-resource stability is not the only determinant of genetic variation. Moreover, trophic-resource stability is difficult to estimate; the Valentine and Ayala estimates are based on diversity gradients in the major adaptive zones—shelf benthic, deep-sea, and pelagic. Many other parameters, potentially capable of affecting levels of genetic variability, correlate with zonal or latitudinal gradients. For example, larval dispersal is not as pronounced at higher latitudes. Dispersal or genetic migration is discussed by a number of authors, among them Crisp and Scheltema, in this volume. It is not clear whether dispersal or trophic stability has the quantitatively larger effect on genetic variation. Phylogenetic relationship also affects the degree of genetic variation, and, as J. P. and J. F. Grassle point out, the most convincing evidence for the trophic-resource-stability hypothesis comes from Valentine and Ayala's study of krill in the genus *Euphausia*. The Grassles' studies of sibling species of polychaete worms of the genus *Capitella* show that genetic variability is related to dispersal ability and population stability or response time in the aftermath of stress. Again, although in a broader sense than that of Ayala and Valentine, it is suggested that genetic plasticity is related to environmental heterogeneity. The Grassles' work as well as that of many others makes the need for careful life history and phylogenetic studies obvious. Electrophoretic tools are useful here, but they are no substitute for lengthy field studies and careful husbandry.

A different, but complementary, approach to the question of genetic variability is taken by those workers who are attempting to correlate single-enzyme-parameter estimation in vitro with field studies. An interesting example of this approach is Siebenaller's report on his study of the electrophoretically inseparable lactate dehydrogenases (LDH's) of *Sebastolobus altivelis* and *S. alascanus*. Although the adults of the two species occur in the same geographic areas, they have different bathymetric distributions; *S. altivelis* is found between 550 and 1300 meters whereas *S. alascanus* is found between 180 and 440 meters. No trend of electrophoretically detectable variation in the other loci studied was found to correlate with depth. However, the apparent K_m's of the LDH's were different under hydrostatic pressure typical of the environment of the deeper-living fish. The affinity of *S. altivelis* LDH for pyruvate is not affected at 68 atmospheres, but *S. alascanus* has a lower affinity for pyruvate at this hydrostatic pressure. The two LDH's have apparently diverged functionally without diverging electrophoretically. The *S. altivelis* LDH is eurytolerant; that is, a single form of the enzyme functions over the entire depth range. This is the strategy suggested by Ayala and Valentine for organisms that occupy environments of low trophic-resource stability. In contrast to this strategy of eurytolerant monomorphism, Koehn presents a case for a polymorphic adaptive strategy at the leucine aminopeptidase locus in the mussel *Mytilus edulis*. *Lap* phenotypes exhibit significant activity differences in high- and low-salinity populations. The frequency of the allele with the highest activity is highest in normal-salinity populations, and these populations exhibit a generally high level of enzyme activity. The converse is observed in low-salinity populations. An understanding of the manner in which natural selection might act at the *Lap* locus to effect adaptation is, however, dependent on a more thorough understanding of the physiological role of this enzyme.

Electrophoresis was used in taxonomy before it was used in genetics, but it has not been widely employed in the former, although a number of statistical measures for quantification of interspecific variation have been developed. Campbell's electrophoretic study of the marine gastropod *Thais lamellosa* confirms its classification as a single, highly polymorphic species. Although some populations exhibited marked divergence, the value Campbell found for Nei's *I* was generally above 0.90 for pairwise population comparisons. No associations of genetic divergence with geographic patterns or environmental parameters were detected. This absence of pattern is, however, consistent with the relatively well-known life history of this snail, which permits the maintenance of small, isolated populations. Thorpe, Beardmore, and Ryland briefly review the ranges of genetic differences reported in studies of conspecific, congeneric, and intergeneric populations. As was first pointed out by Nei, the sampling errors involved in such comparisons are large and depend on the class and number of loci examined. Thus it comes as no surprise that these authors' study of intergeneric distance in bryozoans shows that some *Electra pilosa* and *Membranipora membranacea* are more closely related than some species pairs within the genus *Alcyonidium*. Similar situations are already known in other organisms and many more are surely forthcoming. The available electrophoretic evidence on taxonomic differences shows wide variation among taxa, especially at the specific level. Some species pairs show virtually no allozyme differentiation whereas others differ more than some genera. This suggests that allozymes are no more the full answer in species classification or speciation studies than they are in studies of adaptation. For example, King, Wilson, Nevo, White, Valentine, Campbell, and others have interpreted low genetic divergence among some taxa as evidence for the importance of chromosomal or regulatory changes in evolution. Others have provided evidence of regulatory-gene-mediated adaptation; for example, McDonald has reported increases in alcohol dehydrogenase in *Drosophila melanogaster* adapted to high-alcohol environments. Surely some of the variation in degree of genetic divergence is attributable to sampling error; many, however, suspect that much of the variation reflects real differences in modes of speciation and adaptation.

Only a single paper in this volume deals specifically with chromosome evolution. Colombera and Lazzaretto-Colombera review and present much new information on chromosome numbers and morphology in echinoderms, tunicates, and copepods. Chromosomal evolution appears to have followed different paths in these three groups. The echinoderms show numerical constancy but considerable variation in size and form. Tunicates exhibit variability in both number and form, and copepods show considerable morphological uniformity and low chromosome numbers. In all three groups highly specialized species are characterized by relatively low chromosome number, high chromosome symmetry, and uniformity of dimensions. As specialization/adaptation is organismal, it seems that electrophoretic and chromosomal studies of specialization might be profitably compared, especially in groups such as the copepods, where work in both areas is in progress.

Marine biologists unfamiliar with the electrophoretic literature will find much of interest in this collection, which with some digging conveys not only experimental results but also some of the flavor of more than a decade of rapid and frequently perplexing discoveries. Unfortunately the price justifies purchase only for those small libraries or marine laboratories that do not hold the journals in which most of the material contained in the volume has appeared.

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Extrachromosomal Genetics

Organelle Heredity. NICHOLAS W. GILLHAM. Raven, New York, 1978. xvi, 602 pp., illus. $49.50.

It has now been 70 years since Correns and Baur found genes in the cytoplasm that do not obey the laws of Mendelian genetics. The study of cytoplasmic genes accelerated in the 1950's with the use of microbial systems (*Neurospora*, yeast, *Chlamydomonas*); it took wing in the 1960's with the discovery of DNA in mitochondria and chloroplasts. The last decade has seen the study of organelle genes become one of the fastest-flying fields of genetics, thanks to the combination of sophisticated molecular techniques with unique kinds of mutants and genetic analysis. *Organelle Heredity* is a careful and thorough record of most of the main lines of progress in the field.

It is now clear that eukaryotic cells carry two distinct genetic systems, three if they are photosynthetic. The DNA molecules in the mitochondria and chloroplasts are viruslike, carrying only a few genes relative to the vast number in the nucleus. But the absolutely indispensable role of those genes in the manufacture of the respiratory and photosynthetic systems gives them an importance far beyond their numbers. A detailed understanding of the structure and function of such genes lies not too far away; the mitochondrial DNA of yeast in particular provides an unusually tractable system for detailed mapping at the molecular level and may shortly become known (and perhaps even understood) in an amount of detail rivaling that of our knowledge of viruses. Questions of general interest for students of cell biology and genetics arise at every step. Why are some components of mitochondria and chloroplasts coded by the organelle genes and made inside the organelles while others are coded by nuclear genes and imported? How are the multiple genetic systems controlled and made to function in concert although they are inherited with relative independence? Why are the organelle genetic systems essentially population systems, with tens or hundreds of identical molecules in each cell, while the nuclear genome is haploid or diploid? How and why are genes in mitochondria and chloroplasts so often inherited from only one parent, and why do they segregate during vegetative reproduction, while the nuclear genes in the same cells are inherited biparentally and segregate only during mitosis?

Gillham, a leader in the field, has carefully described the observations and experimental evidence relating to these and other questions about the structure, function, and behavior of organelle genes. There is a wealth of experimental detail, nicely illustrated with graphs, diagrams, and well-printed electron micrographs. Especially useful are tables summarizing data such as the sizes and coding capacities of organelle DNA's of various organisms. There is also careful explanation: experimental methods are explained and evaluated, and the life cycles and husbandry of the principal experimental organisms are described. A modest background in cell biology and genetics will permit graduate or advanced undergraduate students to follow the presentation, although it is not really easy reading because of the detail and the broad scope. The literature is reviewed through 1976 on most topics and through 1977 on some; I know of only a few important papers that have been overlooked. It is a measure of the virtues of the book that I can look with confidence to it for a review of many areas rather than having to wade through my reprint file. It is unfortunate that the price will tend to limit the book to library use, for it deserves to be on the bookshelf of everyone interested in the field.

Though the coverage in the book is broad, it is a bit uneven. Transmission genetics and genome structure are given somewhat more space than organelle biogenesis; the book has more of the flavor of genetics than of molecular biology, although the field itself is at the moment dominated by molecular techniques such as cloning, restriction analysis, and sequencing. It is unfortunate that Gillham's literature review ended just as a great burst of activity with these techniques began. The reader will need to supplement *Organelle Heredity* in this area; the forthcoming collection of papers from the 1979 symposium on extrachromosomal DNA sponsored by ICN Pharmaceuticals, Inc. and UCLA would be a nice introduction to the newer discoveries, such as split genes and restricted codon usage in organelle genomes. A few topics, for instance the experiments on petite mutagenesis, seem to me to have been allotted more space than is justified by their information content. Where there is controversy, Gillham's treatment is scrupulously fair. Some experiments and hypotheses are described and then shown to be false in the light of later observations; this takes up space that might have been profitably devoted to other topics, but at the same time it gives the reader a better feeling for the development of the field and enables Gillham to teach some valuable lessons about the experimental pitfalls lying in the path of the unwary.

Gillham is probably wise to have omitted discussion of the evolutionary origin of organelles; the symbiont hypothesis that has captured the imagination of many has been thoroughly covered in many other places. Also omitted is any discussion of organelle evolution; that is a topic of growing interest (organelle DNA turns out to be an excellent molecular clock and clue to phylogenetic relationships), but some of the best experimental work appeared after the book was written and the theory of organelle evolution and population genetics is still rudimentary.

The book begins with an excellent introduction that summarizes most of the major themes, concepts, and questions of organelle gene heredity and function. Each chapter or group of related chapters ends with a summary of the main conclusions and speculations about likely directions for future work. Some of the predictions have been realized since the book was written, a tribute both to the rapid movement of the field and to the clarity of the author's vision. Gillham is if anything too cautious about making the sorts of generalizations that, even if they failed to stand the test of time, would help the reader tie together the great mass of information and theory. This caution and the organization of the book around experimental systems rather than problems give it a strongly phenomenological flavor. Nevertheless, Gillham has succeeded admirably in his aim to produce a worthy successor to Ruth Sager's *Cytoplasmic Genes and Evolution*; his *Organelle Heredity* is likely to be the standard reference for many years.

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