

ent data to the conclusion that gene activity in differentiation is controlled by a hierarchy of binary switches in which particular genetic loci play a decisive role. Mutants at these loci have homoeotic effects, and their influence is spatially restricted by the same clonal boundaries that define compartments. Kauffman's formalization of this model as an "epigenetic code" is stimulating and raises many new questions concerning the mechanism of translation.

The book achieves a nice balance between theory, experiment, and interpretation. Avoiding a molecular approach, it nevertheless points a way toward one. It will be of interest to geneticists and practicing developmental biologists, and for the most part its ideas will be accessible to advanced undergraduates.

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Silurian-Devonian Paleobiology

Evolution and Extinction Rate Controls. ARTHUR J. BOUCOT. Elsevier, New York, 1975. xvi, 428 pp., illus. \$42.50. Developments in Palaeontology and Stratigraphy, 1.

A. J. Boucot is widely known for his prolific studies of Silurian and Devonian brachiopods. From his long experience with these fossils he has developed the hypothesis that rates of evolution are governed primarily by population size. The larger the population the slower the rate of evolution, whether it is assessed by phyletic, cladogenetic, morphologic, or (what Boucot chiefly employs) taxonomic criteria.

In order to support and elaborate this hypothesis, Boucot explores the brachiopod associations and distributions of the Silurian-Devonian interval. He has written a sweeping description of their ecological and biogeographic units, with special attention to their changing patterns through time. These data are summarized in maps and figures that include a number of range charts containing phylogenetic interpretations. Rates of extinction and diversification and changes in levels of taxonomic diversity are calculated on a stage-by-stage basis. Appendices contain such systemic descriptions and stratigraphic notes as are necessary to document new or unusual taxonomic practices. The treatment is worldwide in scope, although restricted to level-bottom, nonreef associations. Well over half the book is devoted to these matters.

Thus we are provided with a large-scale account of biotic patterns during about 100 million years of Paleozoic time. Silurian-Devonian time embraces some important events in the history of marine invertebrates. Two major waves of extinction occur, one near the end of the Silurian and quite an extensive one near the end of the Middle Devonian. These have never been well explained, but Boucot makes it clear that the second, at least, is associated with a decline in the number of provinces. Also during this time interval, North America and northern Europe were joined after having been separated by an ancient ocean. Boucot has chosen not to consider the effects of continental drift; consequently, distributional data are discussed in terms of modern geography, and the environmental effects of drift are not explored. However, the data will be of use to those wishing to attempt reconstructions with paleogeographic verisimilitude. In any event, the major conclusions drawn from these data are that widespread brachiopod species (assumed to have large populations) tend to persist longer and to evolve more slowly than more narrowly distributed ones (assumed to have small populations).

The remainder of the book is devoted chiefly to factors that control population size, to problems of population size estimates for fossil species, and to factors that might affect evolutionary rates. Discussions are drawn partly from Silurian-Devonian situations and partly from theory, and the theoretical discussions are based chiefly upon recent papers that have been particularly influential or controversial. The topics they take up include the effects of nutrients, biomass, diversity, trophic position, competition, and predation upon evolutionary rates. The discussions are heavily weighted against hypotheses that interpret evolutionary rate regulation in terms other than population size. Thus the stimulating models of Bretsky and Lorenz on mass extinctions are especially singled out for criticism, and the model of the peripheral origin of novel morphologies presented by Eldredge and Gould is reinterpreted as a case of the rapid evolution of small as compared to the slow evolution of large populations.

In the end, this portion of the book is unsuccessful. The most we are left with is the probability that widely distributed taxa usually endure longer than more narrowly distributed ones. We are never presented with a mechanism to account for this difference. Boucot asserts that biologists have developed evidence that evolution proceeds more rapidly in small than in large populations. He mentions the rapid speciation of taxa isolated on islands, presumably attributing this chiefly to their small popu-

lation sizes rather than to effects of the isolation of founder populations in novel environments. Whether island species continue to evolve rapidly is not considered, fluctuations in population sizes are not considered, and the classic treatments of population size effects by Sewall Wright are not mentioned. So far as I am aware, biologists have not in fact presented evidence that populations of the rather large sizes represented by Boucot's "small" populations, which may have distributions that are subcontinental in extent, do evolve faster than even more extensive populations.

Why then do the more narrowly ranging taxa have shorter fossil records? Is it because more restricted taxa are least likely to be discovered in fossil form and therefore tend to have shorter recorded durations? Or do taxa with widely distributed populations tend to be more flexibly adapted, so that they weather environmental changes that carry off narrowly adapted forms with smaller ranges? Such questions are still open. This book is not satisfying as a treatment of evolution and extinction rate controls. Nevertheless it can be especially recommended for its broad coverage of the interesting Silurian-Devonian level-bottom benthos.

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