Book Reviews

Angiosperm Evolution

Flowering Plants. Evolution above the Species Level. G. LEDYARD STEBBINS. Belknap Press of Harvard University Press, Cambridge, Mass., 1974. xviii, 400 pp., illus. $18.50.

The mysterious origins of the angiosperms and the development of their patterns of diversification have fascinated biologists for over a century. In this important and stimulating volume G. Ledyard Stebbins, perhaps the leading contemporary student of plant evolution, applies his extensive knowledge of genetics and developmental biology, together with a lifetime of experience in the field, to these knotty problems. He has been unusually successful in shedding new light on the issues involved and, by carefully outlining the bases of his hypotheses, has made it simple to appreciate the lines of his arguments and therefore to test them in the light of new information or alternative interpretations of established facts.

Stebbins begins with the principle of genetic uniformitarianism, which states that the processes of evolution have operated in the past essentially as they do now. This implies that the origin of major categories was controlled by the same kinds of factors as those now seen to be important in adaptive radiation at lower taxonomic levels. It follows that archaic forms—those which most closely resemble the putative ancestors of major taxonomic groups—are most likely to be preserved under conditions that have been least favorable for the origin of new taxa. The tropical forest is therefore seen as a "museum" rather than a "cradle" for archaic angiosperms. Transspecific evolution may be studied best by focusing on differences between lower-level modern groups that are analogous to the differences between the major taxonomic groups and on the conditions under which such differences arise.

Stebbins argues that the way in which a population will respond adaptively to a changing environment depends to a large degree upon the adaptations that it has already acquired as a result of previous adaptive radiations. He discusses the nature of critical adaptations in plants, distinguishing those associated with adaptation of the individual plant to its immediate surroundings, those associated with pollination and fertilization, and those associated with seed development and dispersal and seedling establishment. One of the crucial concepts in the book is the emphasis on the total lack of connecting forms between major groups among living plants, and the necessity therefore of basing arguments about phylogeny on analogy rather than on the arrangement of living forms in so-called phylogenetic series.

After chapters on gene action and development and the recognition of direction in evolutionary trends involving various kinds of characters, Stebbins convincingly presents the argument that evolution is and has been most active in climatically intermediate regions comparable to those parts of the world that have a mediterranean climate at present. Unfortunately, we have little information about patterns of speciation and diversification in tropical plants, and the urgency of carrying out such studies, in the light of their theoretical importance, is implicit in the book. In view of the worldwide extreme reduction in tropical lowland forests which took place in the Pleistocene, it appears doubtful to this reviewer that low rates of extinction and of differentiation actually characterize most woody plants of these forests; at any rate, the facts are simply not available to evaluate this situation. Nevertheless, Stebbins's contention that seasonally arid habitats are and have been of great importance in the adaptive radiation of angiosperms merits careful consideration, and the matter is extensively discussed in this book. The fact that such arid habitats would have been extensively developed at the time of initial radiation of the angiosperms in the great supercontinent of West Gondwanaland, formed by the union of Africa and South America, has been stressed by Axelrod and others.

Early angiosperms are postulated to be low-growing shrubs, having spirally arranged simple leaves, with bisexual flowers of moderate size probably in a loose, leafy cymose inflorescence. Stamens are thought to have originated from a dichotomous branching system, not from large flattened sporophylls, and extensive arguments are presented in favor of this hypothesis. Another argument that deserves serious consideration is the attempt to establish homology between the ovules of angiosperms and the cupules of the advanced seed ferns, particularly the Caytoniales. If this argument can be sustained, one of the most important questions concerning the nature and origin of angiosperms will have been settled.

The book concludes with discussions of adaptive radiations of many kinds in the angiosperms, including the problem of origin of the monocotyledons. These, like the angiosperms themselves, are seen as monophyletic and derived from the dicotyledons, but with no extant connecting links. Several apocarpous groups of monocotyledons are considered to be archaic and without living intermediate forms. The first ancestors of monocots are seen as rosette-forming herbs, having elliptic, entire leaves (not phyllodes!) with the beginnings of parallel venation. They may have grown on the moist shores of streams and lakes. From them were derived the earliest monocots, in seasonally moist habitats, these subsequently giving rise to the diverse and only loosely interconnected assemblage that survives at the present day.

In his concluding chapter, Stebbins points out several promising directions for future research pertaining to transspecific evolution. Certainly many of the principles of physiological and physical ecology could be applied more extensively to these questions even now. As the basis for understanding development becomes increasingly molecular, more profound comparisons and phylogenetic interpretations will become possible. The architecture of both leaves and pollen, being well investigated currently by a number of workers, will become increasingly important. The paleontological record of both leaves and pollen, if correctly interpreted, is probably considerably better than Stebbins implies. In a world that for most organisms is primarily olfactory, plant biochemistry must yield a great deal that is of high significance in the future,

but only, as Stebbins correctly emphasizes, when a great deal more is known about the biosynthetic pathways involved. Mycorrhizae doubtless control the distributions of many plants, and should continue to be investigated in detail. A new synthetic theory of plant population biology which is now being constructed by ecologists, geneticists, biochemists, and mathematicians will one day help further to illuminate these traditional questions.

By focusing on the adaptive nature of important evolutionary shifts in plants, Stebbins has given us a series of stimulating and well-presented hypotheses, comparable to those which have proved so fruitful in zoology, for study and evaluation. Many students of angiosperm phylogeny have dwelt at such length on the relationships among extant groups and their possible bearing on questions of mid-Cretaceous evolutionary shifts that we have often been unable to see the forest for the trees. In the present volume, a master of evolutionary theory has outlined some of the concepts that may help to free us from some of the more deeply rooted typological concepts of the past and allow us to begin charting with increasing accuracy the actual outlines of the forest.

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A Southern Continental Island

Biogeography and Ecology in Tasmania. W. D. WILLIAMS, Ed. Junk, The Hague, 1974. x, 498 pp., illus. + loose map. Dfl. 140. Monographiae Biologicae, vol. 25.

The importance of the rich biota of the mountainous, well-watered island of Tasmania remains generally unappreciated by both biologists and Tasmanians. Only in the past decade have Australian biologists begun to study the area intensively. This valuable reference volume, which surveys much of the recent work, should help to bring Tasmania into the mainstream of thought on the biology of islands.

The flora of this large continental island comprises over 1250 species of seed plants, including the notorious "horizontal scrub," the only redwoods in the Southern Hemisphere, and the tallest (98 meters) hardwoods in the world. The fauna, with which this volume is largely concerned, includes evolutionary relics like the syncarid crustacean *Anaspides* and geographic relicts like the marsupial "wolf" or thylacine, which is now "very rare or extinct." Some elements of the fauna (marsupials, leptodactyloid frogs, galaxiid fish, and certain arthropods) show strong "Gondwanaland" affinities; other elements (reptiles, earthworms) do not. Endemism and diversity are relatively high. The presence of 48 endemic earthworm species constitutes a species density rarely equaled elsewhere in the world, although it is paralleled on the adjacent mainland, where the world's largest (3.4 meters) worms may still be heard.

This volume contains contributions by 16 workers. It opens with a brief account of the Tasmanian environment and a review of Pleistocene glaciation and subsequent geomorphic history. There are three chapters of primarily ecological interest (on limnology, population ecology of introduced fish, and geographical ecology of the avifauna) and nine detailed accounts of various groups of oligochaetes, crustaceans, and vertebrates. The systematics, distribution, ecology, behavior, and evolution of these groups are treated authoritatively and much new information is presented. Most of the contributors consider the fauna of the adjacent mainland together with that of the island. In his account of the Australian earthworms B. G. M. Jamieson provides a concise review of world oligochaete systematics and a critical analysis of the roles of continental drift and migration in establishing present distribution patterns. There are also reviews of marine littoral biogeography, aborigines, and conservation. A useful companion to this well-produced volume is the separate topographic map. The volume is less comprehensive than some of its predecessors in this respected series. The lack of comparable accounts of other organisms is lamentable (such an account is not yet feasible, according to the editor). More unfortunate for the general reader is the absence of a synthesis or overview of the importance of the biota.

Aside from the intrinsic interest of its biota there are several reasons why Tasmania merits global attention. First, as Williams shows in his discussion of the crustaceans, the island is of signal importance in solving the type of phylogenetic and biogeographic problems posed by groups of organisms restricted to the southern end of the world. In this connection, it is worth noting the difficulties faced by systematists working on these widely disjunct biotas; their important work could be greatly speeded up if there were more opportunities for scientific exchange between the various nations involved. Second, as this volume demonstrates, this area has great potential as a natural laboratory for ecologists, evolutionary biologists, and those interested in extending biogeographic theory to continental areas.

As evolutionary biogeographers begin to tackle the problems of continents the study of their fringing islands becomes increasingly important. Unlike oceanic islands, which are colonized across water gaps, continental islands like Tasmania were repeatedly connected with the adjacent mainland when glacioeustatic fluctuations lowered sea levels during the late Cenozoic. (In the case of Tasmania a broad Bassian Isthmus emerged whenever sea levels fell 65 meters.) The elegant theory developed to account for the biotas of oceanic islands is not directly applicable to continents or continental islands, where the roles of geographic history and coevolutionary interactions cannot be ignored. These variables are more tractable in the case of continental islands, as the contributions of vertebrate zoologists to this volume indicate. Their discussions of geographic speciation, divergence in isolation, species diversity, invasibility, and niche shifts will interest many readers and demonstrate the potential of this area for further studies.

The final chapter of this volume concerns biological conservation. "The Tasmanians have an evil record at this sort of thing," wrote the great Australian zoologist A. J. Marshall in *The Great Extermination* (Heinemann, 1966, p. 216). The record includes the genocide of the Tasmanian aborigines and the eradication of the thylacine. In 1950 a quarter of a major national park was alienated for logging; forest destruction continues today as large tracts are converted into wood-chips for export to Japan. We can only guess what fine Australian expletive Jock Marshall would have used had he lived to see the destruction of Lake Pedder by the Tasmanian government's Hydro-Electric Commission in 1972. Situated in its own national park in the remote southwest, this unique lake, conservation of which was recommended by the International