Taxonomy Phytogeography and Evolution

edited by D. H. Valentine

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D. H. Valentine

Department of Botany
The University
Manchester, England

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Preface

The idea of this conference was first suggested at a meeting of the Linnean Society. It was subsequently developed at a meeting of the Botanical Society of the British Isles, and later discussed at a meeting of the International Organisation of Plant Biosystematists held at Corvallis, Oregon, after the last International Botanical Congress.

To harmonize the aims of all three societies was a difficult task; but it was felt that the attempt was worth making, and a programme with a geographical theme was devised. The reaction of the speakers, all of whom were invited, was encouraging; and the Conference took place at the University of Manchester on September 9–11, 1971. This book presents the papers more or less as they were delivered and approximately in the order in which they were given. The main exception is Professor Kornaś's paper, which was written for the Conference, but could not be presented, as the author was called away to Zambia, and could not manage to travel back to Manchester in time. Nevertheless the paper is an important link in the proceedings of the Conference, and is included in its proper place. Dr. Jardine's paper was given, informally, as an evening talk, but is properly included as a full paper.

The sessions were chaired by Professor A. R. Clapham F.R.S. (Vice-President of the Linnean Society), Mr. David McClintock (President of the Botanical Society), Professor Harlan Lewis (President of the I.O.P.B.) and by Professor H. Merxmüller, Professor Reed C. Rollins and Dr. J. Heslop Harrison, F.R.S.

It would have been useful to include notes of the discussions which followed the papers. This was impracticable; but Professor Clapham's concluding paper, which includes responses invoked from the audience, deals with some of the points which arose.

The Conference was attended by 200 members and guests from 18 different countries. It was followed by an excursion to Derbyshire, in which moorland, heath, woodland and limestone grassland were visited. During the Conference, demonstrations by members of the Conference were on show in the University Department of Botany.

In addition to the societies named, many people and organizations contributed to the Conference. Financial help from the Royal Society, the Linnean Society and the B.S.B.I. made it possible for overseas contributors to come to Manchester, and this is gratefully acknowledged. I should like specially to thank Mr. J. C. Gardiner, until recently honorary treasurer of the B.S.B.I., who not only nursed the Conference in its formative stages, but also gave additional and very welcome financial help.

Thanks are due to the Vice-Chancellor and officers of the University, who kindly held a reception for the Conference. Dr. C. A. Stace and Miss J. Shore of the University Department of Botany headed the administrative and secretarial organization; the smooth running of the Conference (marred only by two minor crises with the coaches, but much favoured by the sunny weather) was due in large part to their hard work.

Readers of the book must judge if the Conference was timely and the contributions well chosen and arranged. There can be little doubt that geographical aspects of taxonomy and evolution have been somewhat neglected in recent symposia; and the papers given at Manchester certainly bring into focus some important problems of evolution. These problems are on the grand scale, in both the spatial and the temporal mode; and though the time is not yet ripe for a major synthesis, the way towards geographical treatment on a broad basis is beginning to appear.

I should like to acknowledge the assistance given by Academic Press and the prompt and efficient way in which they have seen the book through the press. I must also thank Dr. I. B. K. Richardson for preparing the index.

June 1972 D. H. VALENTINE

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Section I

INTRODUCTION

1 | Introductory Remarks

D. H. VALENTINE

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This conference volume contains contributions from distinguished botanists from many parts of the world—a wide geographical spread which is matched by the range of the papers. Some aspects of the conference theme, it is true, had to be by-passed or are only lightly represented and there were few contributions from geographers or geologists; in fact the emphasis was taxonomic and evolutionary. But in a three-day conference, this restriction was no bad thing, and the discussions ranged widely enough.

My own interest in geographical distribution was first aroused when I attended the lectures of J. C. Willis in Cambridge many years ago. Certainly his views on evolution were not at all Darwinian; but he had gathered together a lot of data in a systematic way and had made a number of generalizations based on those data, which in the field of geographical distribution is not an easy thing to do. In classifying species into wides and endemics, and in demonstrating that in all larger taxa the number of endemic species greatly exceeded the number of wides, he posed questions which are still of fundamental importance. What makes a wide, wide? And why do endemics remain endemic? It is of course clear that wides are often the parents of endemics, which evolve in areas which are called centres of speciation; and it is equally clear that wides themselves must often begin as endemics, and have a centre of origin, from which they are able to spread without losing their individuality. A wide is thus a species which is so well buffered in respect of a series of environments and so well equipped in means of dispersal that, given a favourable opportunity, it can travel, apparently unchanged in essential characteristics, over considerable areas.

It is reasonable to suppose that this pattern of wides and endemics has existed at all times, in the past as well as at the present. A balance is

always maintained and there is an equilibrium; but it is a dynamic equilibrium. Environments are constantly changing, and vegetation and flora are in a state of constant flux, with constant migrations. As this happens, the range of a wide is fragmented and the two parts are separated, perhaps for ever. Some populations may be cornered, as it were, in a restricted area, and develop into a group or series of derived endemics. Here they may remain until they die out; or one of them may conceivably break out and set off along a new path and develop into a new wide. I think it is useful to consider evolution in this way against a very broad geographical background. In particular, we need to know where and how major evolutionary innovations arise. Maybe they are forged in the workshop of the local endemic, and then spread abroad in the form of a wide. Should this chance to meet another "original" wide, a crucial hybridization may occur, and new combinations may be made which are developed and worked out, as it were, in a new crop of endemics, until one of them enters again into the dispersal phase of a wide. These ideas are, I think, particularly relevant in thinking about major evolutionary problems, such as the origin of the angiosperms. One would not expect to find, in the fossil record, more than a few ancestral forms, in any one place; and the new evolutionary discovery may have been worked out, along somewhat different lines, in more than one geographical area.

In the papers presented at the conference, authors have considered, on the one hand the very large geographical areas, with their wides and series of vicariant taxa, and on the other hand, the smaller, more circumscribed and more or less isolated areas, in which clusters of endemic species have arisen. Both types of situation give rise to many problems, both taxonomic and evolutionary. A feature of geographical studies in the middle part of this century has been their investigation by biosystematic methods and the application to them of biosystematic concepts. It has thus become possible to study the flora of an area in a new way which is not entirely taxonomic, nor entirely chorological, but which combines the two with cytological and genetic information to form a comprehensive synthesis. A pioneer study of this kind was that of Á. and D. Löve (1956) on the flora of Iceland, itself based on the earlier paper of Á. Löve (1954) on corresponding taxa, and on the concepts of gradual and abrupt speciation (Valentine, 1949). These ideas have been developed in a number of ways, some of which are described in the Chapters below.

The general arrangement of the programme at the meeting was fairly straightforward. The first contributors looked mainly at evolution over major geographical regions, and wides were often the subject of discussion. Then the emphasis moved in the direction of endemics, and there were discussions of migration of both wild and cultivated plants. A third main topic was aspects of evolution and phytogeography in large or well-studied genera, including at least one apomictic genus. Papers on chorology, that is, on the classification of species into floral elements on a geographical basis, were unfortunately few in number. It was hoped at one time to have more papers of this kind but, for various reasons, the number had to be reduced. It is particularly regretted that it was not possible to have an up-to-date account of the chorology of the British Flora, which is now so well-known and well-mapped. As some compensation for this, the inclusion of Dr Jardine's contribution (given as an evening lecture) introduces some of the problems associated with the new techniques of computer mapping and analysis; accurate data on geographical distribution and efficient mapping are at the basis of discussion on phytogeography and evolution. An important project that might be mentioned here is the mapping of the whole European Flora, which is being organized by an International committee, based at the University of Helsinki.

Finally I would like to add a word about the sponsorship of the meeting. Three societies joined together as sponsors; much the oldest of these is the Linnean Society of London, famous for its Linnean collections, and its meetings at which biologists of all kinds can come together to discuss current theories and discoveries, particularly in the field of taxonomy. The Botanical Society of the British Isles can also boast a respectable history, going back in one form or another for more than a hundred years. As its title implies, its scope is less wide than that of the Linnean Society, but it, too, is famous both for the great skill of its members, especially its amateur members, who nowadays flourish perhaps more strongly than ever, and also for its increasing interest in modern developments in taxonomy and phytogeography. Last, and certainly the newest of the sponsoring societies was the International Organisation of Plant Biosystematists. It is only ten years old, and it has not yet produced a journal of its own, but through its occasional publications, its conferences and its world-wide membership, is able very effectively to promote the study of plant biosystematics. All three societies were represented at the meeting by their president or past-presidents; and in welcoming them and

their members to Manchester, I expressed the hope that their co-operation would be fruitful and continuing.

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2 | Ecological Distribution of Centers of Major Adaptive Radiation in Angiosperms

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INTRODUCTION

Geneticists and cytogeneticists concerned with the processes of evolution, with few exceptions, have confined their attention to the level of populations and species, and have paid little attention to evolutionary trends at the level of genera, families and higher categories. This focus is justifiable, since the problems of evolution above the species level cannot be attacked directly by experimental means. Nevertheless, plant evolution as a whole will never be understood until botanists become able to find out whether or not major trends of evolution can be entirely explained on the basis of processes that can be observed and studied at the level of populations and species, and if they can, what kinds of projections or extrapolations are necessary to establish connections between micro- and macroevolution.

The present discussion is based upon the hypothesis that evolution at all levels is guided by the same kinds of processes, and that the proper study of macroevolution is one that differs from experimental investigations of microevolution only in degree, with different emphasis placed upon certain aspects of the study. The macroevolutionist must place greater emphasis upon historical events, particularly the differences between past and present environments and consequent distributional patterns of biota; as well as extinction of formerly dominant floras. Furthermore, he can profit from the experimental method only by making certain assumptions. The first and most important of these is an hypothesis that can be called *genetic uniformitarianism*, since it corresponds to geological uniformitarianism, as this concept was first put forward by Hutton and Lyell, and formed the basis of the historical aspects of Darwin's theory.