Contacts between Plant Classification and Experimental Botany*

By Dr. W. B. Turrill

TAXONOMY, from the Greek origins of the word, is the law of order. The theory and practice of classification is, and has been, the first function of the taxonomist. In the earlier history of botanical taxonomy the theory was based primarily on the dogmas of the creation and fixity of species, and this tended to the codification of artificial laws for classifying the taxonomic units, with the practical aim of easy and certain identification. With the acceptance of evolutionary ideas, the theory has largely changed, and with this change other applications have appeared and sometimes confuse results. The dogma of the constancy of species had at least one advantage for the taxonomist—his work was simply the classification of theoretically clear-cut units. Nowadays, the dynamic point of view is in vogue, and phylogenetic considerations are sometimes allowed to dominate the practical issue of classification. How far supposed phylogeny can be used advantageously in classifying the larger plant groupings is not a subject-matter of this paper; but there is a danger that classification for utilitarian purposes may be subordinated to classification for the sake of theoretical considerations.

Owing largely to the broad training which is now generally given to botanists in schools and colleges, the number of professional botanists who are content merely to identify, describe and classify on the basis of gross morphology is being reduced. It may, indeed, be suggested that a static system of endless descriptions would kill taxonomy. Many systematists give a phylogenetic flavour to the dishes they set before their colleagues. Phylogeny, to be real, must lead to a consideration of genetical problems, and the taxonomist immediately comes into contact with experimental work. Or, the taxonomist becomes keenly interested in the distribution of the plants with which he works, and modern phytogeography naturally links up with ecology and with many of the ecological problems which can only be solved by experiment. My object here is to discuss those contacts with genetics and experimental ecology which can lead to improved taxonomic technique and results, and perhaps to radical changes of outlook. It should, however, be expressly stated that no derogatory criticism is made of those taxonomic methods which are now in general use, except to emphasise their limitations. A working taxonomist knows only too

well how much yet remains to be done by the older methods, the usefulness of which will probably never be exhausted. There are, however, many essentially taxonomic problems which cannot be solved by comparative morphology alone, and taxonomists have a duty to their science in directing the attention of their genetical and ecological colleagues to these.

Exact identification of the material used is, or should be, a first consideration in biological experiments. A geneticist or ecologist who does not ask for and use the advice of a systematist runs chances of such error as may make his work not merely useless but even misleading. There are, then, so many occasions on which the taxonomist and experimental botanist can co-operate with reciprocal advantage, that the wonder is that more attempts to understand each other's problems have not been made. A plea is here put forward, from the taxonomic point of view, that geneticists and ecologists will undertake problems the solution of which will materially assist the taxonomist. It is convenient to consider some of these problems under two broad heads—genetical contacts and ecological contacts.

GENETICAL CONTACTS

Genetics, it is interesting to remember, commenced as an experimental science, and though it is now inextricably linked with mathematical formulæ and with observational cytology, it still retains the living plant or animal as its basic material. Genetical experiments in plants have a simple fascination for the taxonomist in that a considerable number of living individuals, grown under uniform conditions, can be studied comparatively. The importance of studying living material is often forgotten by herbarium workers, just as the importance of herbarium material is often ignored by experimentalists.

There are, however, contacts more peculiar to geneticists and taxonomists. The establishment of a phylogeny on an objective basis depends fundamentally on palæobotany and, for the smaller taxonomic groups, on genetics in the broad sense. If the morphologist arranges a group of organisms in a linear sequence, he can only suggest very tentatively that the sequence is phylogenetic and which way it should be read. If he makes a radiating or branched diagram to illustrate his theories, the results cannot, in the absence of

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palaeobotanical or genetical data, be considered as more than possibly true. Perhaps the work of Prof. Babcock and his colleagues on the genus *Crepis* best illustrates how genetical, and especially cytogenetical, studies can control phylogenetic speculation.

The taxonomist has one constantly recurring problem, that of evaluating characters, and on the evaluation subordinating one taxonomic group to another, or, alternatively, equating them. Put simply, this usually means, shall he consider *A* and *B* as distinct species or as subspecies or varieties of one species? Similar problems of genera and subgenera, etc., occur among the larger taxonomic groups, but are less amenable to experimental treatment than those at the species to variety levels. This problem has received very little deliberate treatment by modern methods. My own experience and the published results of geneticists with which I am acquainted, and which bear more or less directly—though usually unintentionally—on the subject, suggest that the kind and degree of morphological difference often give, by themselves, very little indication of how the units should be subordinated on a sound basis of fact. So far genetics has not, by itself, given us as much help as might be expected in determining the relative value of phenotypic expressions of related but different genotypes. Thus within *Silene Cucubalus* or *S. maritima* we find, after twelve years' work, that, with very few possible exceptions, no greater taxonomic value can be given to any one genotype than to any other on the basis of genetical behaviour alone; that is to say, no one varietal character or set of characters can be taxonomically subordinated to any other by its genetical behaviour, except, perhaps, in a few examples of clear-cut dominance. Mere accumulation of different genes gives, as I have shown elsewhere, no satisfactory basis for subordination in classification.

The importance of isolation as a taxonomic criterion can scarcely be exaggerated. Species must be morphologically distinguishable and determinable, but so must varieties. Species, however, must be isolated one from another, otherwise they inbreed to form one polymorphic multivarietal species. The kind and degree of isolation is a wide subject, involving ecological, phytogeographical and other considerations, besides genetical. The taxonomist is most often concerned with wild plants, and it is therefore of great importance to him to know what they actually do in Nature rather than what they can do when brought together artificially. Yet the most complete isolation is undoubtedly complete inability to cross. This inability to cross cannot usually be judged *a priori* on the basis of degree

or kind of morphological difference. Thus Chitenden and I showed that in the genus *Nemophila* some, at least, of what a recent worker has called subspecies and varieties of *Nemophila Menziesii* were not only morphologically distinct but also would not cross even with reciprocal pollinations. On the other hand, some morphological entities, quite distinct when selfed, interbred with full fertility (*Kew Bull.* 1926, 1). In this genus, certainly, the entities completely isolated by failure to cross fit in with the best conception of species, those that inbreed agree with the best definition of varieties. *Centaurea Scabiosa* and *C. nigra* will not cross reciprocally, though they very frequently occur together in Nature; *C. Scabiosa* and *C. collina*, morphologically quite distinct, can be crossed artificially, and produce fertile offspring, though they appear to keep distinct in Nature, owing to other, probably in the main geographical, barriers to interbreeding. The behaviour on crossing of plants belonging to the same species, in that they are not morphologically differentiated, but from populations isolated by discontinuous distribution, is another subject which the taxonomist would suggest for extensive genetical experiments.

The cytological demonstration by Prof. C. L. Huskins of the hybrid origin of the true-breeding *Spartina Townsendii*, and the artificial creation of *Galeopsis Tetrahit* by Dr. Müntzing suggest that hybridisation may be more important in evolution than is yet realised. How far the reticulate connexions between species, genera and families is due to this it is impossible at present to say. The writings of the late Dr. Hayata on the dynamic system of plant classification are often difficult to understand, but that reticulations similar to those of which he gives examples are of very common occurrence in plants is certain, and the failure to account for them or even to consider them is a major fault in most systems of classification that claim to be more than artificial conveniences. We have few general data as to the taxonomic limits within which fertile hybrids can be produced. Intergeneric hybrids in orchids would surely pay for more detailed analysis. This reticulate distribution seen in character combinations at all taxonomic levels (varieties, species, genera and families) may or may not be due to hybridisation having been the major factor in evolution, as the late Dr. Lotsy urged, but it is surely a subject which should be analysed from the genetical point of view. A taxonomist would also like the regular publication of the negative results of genetical experiments. That the species cannot be made to cross may cause the geneticist to lose interest in a genus, but such genetical isolation may have very considerable taxonomic importance.

The taxonomist studying widely-distributed species frequently finds that the intraspecific variation is not only great but also varies in kind and degree in different parts of the distributional area. Such variation must, in view of the specific and varietal criteria already suggested, be of interest both to the geneticist and the taxonomist, and important in the study of both wild species and cultispecies. While the investigation of intraspecific variation and heterozygosity is well advanced for many of the latter, relatively few wild species have been intensively and extensively studied genetically. Wild species must be the only material which can give real proof of the origin of species by, for example, natural selection, and it is surely much better to obtain and use the necessary data from such, rather than to estimate selection by analogy with plants known only in cultivation or by mathematical symbolisation not directly based on experiment.

In his troubled career, the taxonomist meets, or if he be wise, tries to avoid, such genera as *Rubus* in the British flora or *Crataegus* in the North American. The taxonomy of the British genus *Rubus* is in such a state that specialists sometimes cannot agree in more than one determination in ten. It is probable that the usual taxonomic recording is really impracticable in such genera as *Rubus*, and a totally different scheme from that of species and varieties will have to be evolved before stability of expression is reached. Before such can be elaborated, the taxonomist requires data concerning genetical stability, hybridisation, heterozygosity and so on, which can only be obtained by genetical experiment.

ECOLOGICAL CONTACTS

The ecologist studies primarily the relationship between plant-life and environmental conditions. Synecology cannot, of course, be properly studied without a good taxonomic knowledge of the local flora—a knowledge which some ecologists unfortunately do not trouble to obtain. Here, again, the help of the taxonomic specialist should be sought, and it will be the more readily and the more precisely given if the taxonomist obtains in return good sets of specimens for his collections. Synecology, however, is not essentially experimental in method. Autecology is or should be largely experimental, and is very closely related indeed to taxonomy. One can almost say that any autecological fact is of taxonomic importance.

The essential difference between stable (constant) or unstable (inconstant) characters is that, in the former, different environments cause no change when interacting with the same genotype, while in the latter the phenotypic expression of the same genotype fluctuates with the environment. The

degree of plasticity in a given range of different environments is a specific character which cannot be known *a priori* in the absence of experimental evidence. The British Ecological Society's transplant experiments at Potterne have shown very clearly that reaction to soils varies greatly in different species. Thus *Centaurea nemoralis* flourishes almost equally well on the five soil types being used; *Anthyllis vulneraria* shows no change in morphological characters, but different death rates; *Fragaria vesca* and *Phleum pratense* are decidedly plastic, especially in quantitative characters; *Plantago major* is so decidedly plastic that one is forced to conclude that recent taxonomic publications on this and allied species based on herbarium material and without experimental support have little value. Transplant experiments, properly conducted, with full scoring and analysis of data, are slow and time-consuming, but until such are extended to a much wider range of species and of environmental conditions (especially changes in the wide series of climatic factors) the taxonomist has to make rough guesses from meagre observational data.

Another ecological subject of taxonomic importance is the occurrence of habitat barriers between species and also between what Dr. Turesson calls ecotypes. It has already been remarked that the kind and degree of isolation between putative taxonomic units is of the greatest importance in the establishment of an objective classification. Such isolation may be genetical, it is often geographical, and not infrequently it is ecological. Sometimes the isolation is so great (if not absolute) that morphologically distinguishable units are justifiably ranked as species, even if they can breed together to give fully fertile offspring. *Silene Cucubalus* and *S. maritima* are common British plants, each with a distinct ecological range. In the experimental ground they cross readily, and the offspring are fertile *inter se* and with each parent. The two species rarely meet in Nature; natural hybrids are therefore few, and amalgamation of the two species to one does not take place, as it might well do, but for the ecological barriers.

Seasonal dimorphism is of importance to the taxonomist in adding not only to the difficulties of identification but also to those of classification. The late Prof. Wettstein, it will be remembered, stressed its importance in his studies of the genera *Euphrasia*, *Gentiana* and *Alectorolophus*. It is much to be desired that experimental evidence should be obtained on a large scale as to the constancy of development and flowering at different seasons, and the variation in characters with age, especially with age reckoned from the commencement of annual growth, and of the correlation of these with other specific or varietal criteria.

SUMMARY AND CONCLUSIONS

Of the many subjects of common interest to taxonomists, geneticists and ecologists, those mentioned here have, for convenience only, been referred to under the two headings, genetical and ecological. This division is artificial and unsound in practice. It is only when all methods are used, so far as possible on the same material, that taxonomic judgments can have any final value. It can be justly urged that the professional taxonomist is frequently too overwhelmed with the mass of material he is expected to identify and classify to have time to carry out slow time-consuming experiments, even if he has facilities for them. On the other hand, those taxonomists who have had a recent botanical training should have a sufficient grounding in plant ecology and plant genetics to be able to appreciate those ecological and genetical methods and results which bear on their own studies, and should be keen to co-operate with their colleagues. It is also probable that a continual personal acquaintance with experiments on living plants, even if on a small scale, is advantageous to the taxonomist in keeping his outlook broader than it can be with herbarium

routine not merely dominant but absolute. The judicious use of an experimental ground attached to a taxonomic institution pays over and over again in increased interest in major problems and in efficiency in solving taxonomic difficulties.

It may be an overbold thing for a taxonomist to suggest to his genetical and ecological colleagues that, if he were consulted, he could set them problems the solution of which would not only have first-class value in the special domain of genetics or ecology respectively, but would also directly assist the taxonomist. The taxonomist often regrets that relatively so much more genetical research has been concerned with cultivated than with wild plants. He realises the economic reasons for this, but hopes that more research can be undertaken which has not an economic end directly or immediately in view. If botanists with opportunities would undertake intensive studies on small groups of allied species, with a taxonomic ideal but using genetical, ecological and other experimental and observational methods, they would produce work of permanent value, and help to the unity of botanical science.

Obituary

Prof. J. S. Haldane, C.H., F.R.S.

"Il montra que si le physiologiste doit sans cesse recourir aux notions que lui fournissent l'anatomie, l'histologie, la médecine, l'histoire naturelle, la chimie, la physique, il doit en rester le maître, les subordonner à ses propres visées ;" . . .

Thus a distinguished worker in Haldane's own special sphere, namely, Paul Bert, summed up the teaching of another great physiologist—Claude Bernard. The words are no less applicable to Haldane himself, for, remarkable as were his researches and writings on many aspects of pure and applied physiology, their value was founded in his deep insight and his search for a philosophical basis on which he could build up an intelligible interpretation of the phenomena of life, which he saw could only be understood as a whole.

It is a proof of the acuteness of Haldane's insight that, so early as his days as a medical student at Edinburgh, he was not content to accept without inquiry a teaching of physiology which did not satisfy his demands for a consistent description of its various aspects. His impatience with superficiality and desire to penetrate to fundamental conceptions of phenomena lasted throughout his life and found expression in a series of philosophical essays and books, which began with an "Essay in Philosophical Criticism" published in 1883 in collaboration with

his brother Lord Haldane, and culminated in "The Philosophy of a Biologist", 1935. Between these times he never lost his interest in philosophy and, despite the great amount of work he did in pure and applied physiology, found time to write "Mechanism, Life and Personality", 1913, "The New Physiology", 1919, "The Sciences and Philosophy", 1928 (Gifford Lectures), "The Philosophical Basis of Biology", 1931 (Donellan Lectures) and "Materialism", 1932.

Though Haldane always maintained his insistence on the necessity for broad conceptions, he became particularly interested in the physiology of respiration at the very beginning of his scientific work. This interest in respiration led him in turn to another aspect of physiology of which he was a brilliant pioneer, namely, its applications to problems of industrial hygiene. His thoughts perhaps turned in this direction owing to the fact that he became demonstrator at University College, Dundee, under Prof. Carnelley, with whom he carried out an investigation of the various impurities present in the air in buildings and sewers, which was published in 1887.

Soon afterwards Haldane went to Oxford, where he became demonstrator in physiological chemistry under his uncle, Sir John Burdon Sanderson, and where he remained for the rest of his life. Here he soon began the work which led to the publication,