PRESLIA 1962
34 : 207—226

S. M. Walters:

Generic and specific concepts and the European flora

(Botany School, University of Cambridge)

In recent years the output of taxonomic works relevant to the European Flora has greatly increased. At the same time there has been a growing interest in the theoretical aspects of taxonomy, and in the impact on the orthodox taxonomy of modern studies such as cytology, genetics and the variability of populations. This breakdown of the taxonomist's isolation affords an important opportunity for useful discussion which can range over the whole field, from the methods of the herbarium taxonomy descended from the Linnean school to the application of statistical methods employing mathematical computers, from the idea of a species as a type specimen in a collection to the idea of a variable and evolving population in nature. The Flora Europaea project itself could hardly have taken shape in an earlier period, for although the actual Flora being written is quite "traditional" (see HEYWOOD (ed.) 1958 for details), both the Editorial and Advisory Committees contain botanists whose interests are primarily in more modern aspects of taxonomic studies, and the discussions at the Symposium held in Vienna in 1959 (HEYWOOD (ed.) 1960) bear ample evidence of the general interest in the more modern approaches.

My purpose in this paper is to survey some of the literature relevant to modern studies of the European flora, and to attempt to indicate areas of agreement and possible solutions to some of the theoretical arguments about the nature and delimitation of taxa which are taking place as a result of these studies. There is a vast literature and this is not meant to be a comprehensive review. I hope that it will, however, indicate sufficiently well the general areas of development.

History

Logically, a study of taxonomy should begin with a historical survey. It is, however, possible to write history in a bewildering variety of ways, and for our present purpose many historical contributions are of little relevance. There is a very understandable tendency among taxonomists — indeed this probably applies to biologists as a whole — to take their acquaintance with the writings of their predecessors at second-hand from short historical accounts of the subject in standard text-books. This is perhaps excusable on the part of the biochemist or cytologist, for to him the early writings are probably at best only of academic interest; but for the taxonomist the position is radically different. Whether we like it or not, mid-twentieth-century biology is using a system of description and classification for the higher organisms which cannot be understood except as a product of seventeenth and eighteenth-century minds. History cannot be, as it were, an "optional extra subject" for the taxonomist interested in what he is doing and why; for all the tools of his traditional activity go back basically unchanged to the time of Linnaeus, and indeed in some cases to much earlier times. In this connexion the recent publication of a new facsimile of the Species Plantarum, including most valuable introductory and additional material relevant to the understanding of Linnaeus' work, is of major importance, and the work should be consulted by all taxonomists (STEARN 1957, 1959).

Although it is common knowledge, the importance of the fact that modern biology originated in a particular area of Europe (cf. STEARN 1959a) seems to have been very little stressed by writers on the history of taxonomy. The wider implications of a restricted origin in time and space for the shape of modern Angiosperm taxonomy cannot concern us here, and I have dealt with them elsewhere (WALTERS 1961). It is not however possible to understand some of our modern problems concerning genera and species without relating them to this historical background. We must find out who in fact "created" the taxa we still use today, and if possible try to understand both the practical technique employed and (a more difficult task) the thought-processes involved. Although for these purposes a study of the Species Plantarum is valuable and instructive, it is by no means sufficient; for Linnaeus himself was not operating *in vacuo*, and indeed a great many of the really familiar genera of north-west Europe at any rate were already known (i.e. the name and roughly the present concept) long before the time of Linnaeus. TOURNEFORT (1700) or even BAUHIN (1623) can be consulted to verify this. The genus and the species, in many cases even in the familiar "Linnean" binomial, were well-defined concepts widely in use in seventeenth-century biology, and they arise from Aristotelian philosophy, concerned with the nature of classification in general. This philosophical aspect of Linnaeus' work, to which I shall return later, is ably discussed by CAIN (1958).

The two-stage hierarchical classification of genus and species, standardised by Linnaeus, can then be looked upon as a "philosophical necessity" in the growth of biological science. In practice it was strongly reinforced by the effect of rapidly increasing knowledge, which necessitated subdivision of groups already recognised in medieval herbals, often because of their medicinal or other importance in the life of the community. Thus the genus *Gentiana* originates as a name for a kind of plant important for its medicinal properties, and then expands (or fragments) with increased knowledge into a number of different species. Gesner wrote in the sixteenth century (ARBER 1938): "There are scarcely any plants that constitute a genus which may not be divided into two or more species. The ancients described one species of Gentian; I know of ten or more." Or, to take another example of familiar plants, many modern Umbelliferous genera can be traced, as names for kinds of Umbellifers, back to that remarkable work by MORISON (1672) "Plantarum Umbelliferarum Distributio Nova", which is the first family monograph ever written. LINNAEUS did not, in such cases, have a free hand; he was, as we are today, influenced and restricted by the traditional literature; and in many cases where common European plants were concerned, the name and the approximate concept were given to him ready-made.

This fact is of the utmost importance in understanding the shape and size of Angiosperm genera — and indeed of families too, although a consideration of this aspect is outside the scope of the present paper. It enables us to give an answer, in terms of the history of the generic concept, to questions such as: "Why are many Umbelliferous genera small and difficult to define?" or "Why are certain Angiosperm genera such as *Senecio*, *Astragalus*, *Euphorbia* and *Carex* of enormous size?" The key to these problems is to be sought, not primarily in the nature of variation in the group concerned, but in the history of taxonomy. The relevant parts of that history can be summarised as follows:

Description and naming of kinds of plants (pre-Linnean).

Increased knowledge leading to a generic and specific concept (pre-Linnean).

Standardisation of genus and species with binomials; definition (more or less adequate for known material) of genera. (LINNAEUS).

Enormous addition of new material, especially extra-European, using the Linnean framework (late eighteenth century and early nineteenth century).

Slower growth with detailed monographic work; "creation" of small and monotypic genera (mainly second half of nineteenth century).

The thesis here advanced may be summed up in the following generalisations:

1. There is a general correlation between the size of genera within a family and the age of those genera as concepts in the mind of the taxonomist. A similar correlation exists between age and size of families. These correlations were noted by J. C. Willis (cf. particularly WILLIS 1949), but given an erroneous interpretation; he thought of the age of the taxon as its presumed evolutionary age, and failed to see its significance in terms of the history of taxonomy. This correlation requires no explanation not inherent in the growth of taxonomic knowledge.

2. No large genus can be wholly or even largely European. This follows from the fact that the European flora was relatively well-known over many centuries, and genus-forming names would be available to Linnaeus from the earlier botanical literature. Thus the *Umbelliferae* consisted of a family containing a large number of genera in pre-Linnean botany; had they been unknown and undescribed, they might have constituted a single genus. The few exceptions to this "rule" are themselves very illuminating; for example *Silene*, one of the largest European genera, has the main mass of its species in the E. Mediterranean area, relatively unknown to Linnaeus, who had only 27 species in the Species Plantarum (for the whole world !).

3. The really large genera in the world's flora are "old" in concept and so delimited by Linnaeus that large numbers of post-Linnean species could eventually be accommodated in them. The enormous genus *Euphorbia* provides a very instructive contrast to the *Umbelliferae*. In both cases the plants are easily recognised as constituting a group, at least as they are represented in Europe. Both have a rather precise, specialised inflorescence structure, and both possess useful vegetative characters. Early recognition of these general resemblances led, however, in the case of the *Umbelliferae* to the recognition of a family with many genera, whilst *Euphorbia* remained a sigle genus. Here the different pattern of classification has, I believe, its explanation deep in medieval botany, which itself was explicitly based on the Greek writers. The single fact which prevented the pre-Linnean recognition and naming of a number of genera in "*Euphorbia*" was their essential similarity in medicinal use; the different kinds of *Euphorbia* were not importantly different for the purposes of recognition by the herbalists of Europe. This absence of "genus-forming names" meant that Linnaeus tolerated, in the case of *Euphorbia*, a genus of 56 species, the largest genus of flowering plants to be found in the Species Plantarum. The largest genus of all, *Senecio*, in which we tolerate more than 2000 species, contains a mere 27 in the Species Plantarum; a broad generic diagnosis which was adequate for botanical knowledge at the time of Linnaeus has allowed many hundreds of species discovered subsequently to "flow" into this genus.

4. Two main factors led to early recognition of genera in Europe, viz. conspicuousness and economic importance. Thus most familiar European trees belong to different genera, since they combine both these features; and we are therefore obliged to work a generic difference between, say, *Alnus* and *Betula* or *Quercus* and *Castanea* because of the history of pre-Linnean botany. An extreme case where conspicuousness and economic importance combine is provided by the fruit-trees related to the pear (*Pyrus*). Here Linneaus was provided with generic names from the classical authors (*Pyrus*, *Malus*, *Cydonia*), but he was so impressed by the similarity of these

genera that he united them under *Pyrus*. It is particularly amusing to find in this case that tradition has proved ultimately too strong, and we have reverted to the classical genera provided for us. Can we seriously doubt that if the fruit trees of the *Pomoideae* had been, say, New Zealand plants unknown to pre-Linnean botany, we should now have been contentedly operating with a single genus? The *Gramineae* provide an interesting study in the evolution of generic concepts, particularly when the generic pattern of the grasses is contrasted with that in the *Cyperaceae*. Many common European grasses are Linnean genera, (e.g. *Alopecurus*, *Avena*, *Hordeum*, *Lolium*); they are and were of economic importance either as pasture grasses or cereals, and a pre-Linnean monograph of the *Gramineae* exists (SCHEUCHZER 1719) in spite of the technical difficulty involved in the description and comparison of the grass flower and inflorescence. As in other cases, Linnaeus was given ready-made a number of generic concepts in the *Gramineae*. By contrast, the *Cyperaceae*, of similar technical difficulty but lacking economic importance, were relatively unknown to Linnaeus; hence the enormous genus *Carex*, which now has over 1000 species, but in the Species Plantarum contained only 29.

I should perhaps make it clear now that I do not wish to imply that no objectively definable differences exist in patterns of variation within and between groups of Flowering Plants. It is obvious that there are great differences in this respect, and I shall return to a consideration of these later. The single point which must be made here is that nothing can usefully be said of the significance of the different sizes of genera if the origin of the genus as a concept is ignored, nor can discussions on the "reality" of genera and species possibly be useful if conducted in ignorance of the philosophical background of the terms.

The great taxonomists of the late eighteenth and early nineteenth century, de JUSSIEU, de CANDOLLE, Robert BROWN and others, produced the main outline of the system of Angiosperm classification as we use it today, and, beginning with de JUSSIEU's Genera Plantarum (1789), named and defined most of the genera which we still use. It cannot be too strongly emphasised that Angiosperm taxonomy is a wholly pre-Darwinian discipline, both in its practice and in its theoretical justification or philosophical basis. We have an excellent account of these principles of taxonomy in de CANDOLLE's "Théorie Elémentaire de la Botanique" (ed. 2, 1819). For our purposes here, de Candolle's discussion of the genus and the species is particularly interesting. In the second edition he defends the generally held belief in the fixity of species, but shows himself fully aware of infraspecific variation and the problems it raises, recommending experimental procedures to help to decide whether two taxa should be treated as separate species or as mere varieties of a single species. These experiments should involve cultivation and growing the plant from seed, if possible through several generations. Regarding the genus he is extremely practical, giving a series of rules for the creation of genera. These are quite honest and explicit, and even allow, "in doubtful cases", for the use of practical considerations, such as the number of species to be included. "To avoid useless nomenclatural changes, one should", in certain special cases, "leave the genera as it has been customary to have them, and indicate divisions as simple sections". No better advice could be given to mid-twentieth-century taxonomists!

In de Candolle's work we see an interesting difference of emphasis from that of LINNAEUS, who in Philosophia Botanica (1751) stated that both species and genera are natural, distinctly created units:

> "Species numeramus, quot diversae formae in principio sunt creatae".
> "Genus omne est naturalis, in primordia tale creatum".

(It is of course true that LINNAEUS found difficulty in reconciling the existence of hybrids with such a rigid view, and somewhat modified it in a later work.) We find LINNAEUS insisting on the "reality" of both species and genus; de Candolle, whilst clinging to the dogma of special creation and the fixity of species, clearly treats the genus as a classificatory unit to be made, if necessary, on severely practical considerations of convenience to the user of the classification. It seems possible that this difference in emphasis has at its basis the different states of knowledge in the two periods; Linnaeus was inevitably, as we have already seen, occupied to a large extent with using a traditional accumulation of names for more or less well-known plants; whilst de Candolle and his contemporaries took the ordered Linnean framework of genera and species and had to add a vast number of new plants from the hitherto unexplored parts of the world. The "art of genus-making" *de novo* was practised mostly between 1780 and 1850. The new species might be recognised by the explorer-naturalist in the field, at least in a number of cases; but the decisions as to the generic boundaries were taken in Herbaria in Geneva, Paris, Berlin and London.

Logic of classification

We must now consider briefly the subject to which some reference has already been made, namely the inter-relations between logic and philosophy on the one hand, and "natural classification" on the other. An adequate treatment of this difficult subject is not within my power, nor would it be possible to accommodate it in this paper; but the relevance of the general theory of classification to our subject is too obvious to need justification. Linnaeus, as we have seen, based his standardisation of genus and species on the traditional Aristotelian logic. This in itself inevitably took as its main illustrations the classifications of living things, and it seems reasonable to conclude that formal logic, which was an essential part of the mental apparatus of every educated man before the nineteenth century, is, as it were, adapted to the particular requirements of biological classification. Thus the idea of the"kind" as a natural class or grouping of objects sharing an indefinitely large number of common attributes, arose from observation of the world of living beings, in which individuals can be grouped into "kinds" and are in fact so classified, to some extent at least, in ordinary language. In the formal logic familar to Linnaeus, five sorts of class-name are available ("Predicables") viz. genus, species, differentia, propria and accidens. The first two differ in that they must be of the "essence" of the subject; they must be true "kinds"; and Linnaeus was being faithful to the traditional logic in converting this to a belief that both genera and species were created as such. In two respects, however, the Linnean standardisation distorted Aristotelian logic; firstly in that it used the predicables as technical terms for the classes themselves; and secondly (a more serious departure) it restricted their use to make a pair of categories, one subordinate to the other, whereas in logic the same name can be a genus with respect to a subordinate species, and a species with respect to a higher genus.

From the time of Linnaeus onwards, few biologists have been very interested in the logical background of the technical terms — indeed regrettably few seem to have shown much interest in the philosophical basis of classification as a whole — and the significance of the Aristotelian distinction seems to have been rather over-looked. Among the logicians and philosophers, however, J. S. MILL in his System of Logic (1843) gives a remarkable assessment of the theory of natural classification, stressing the value of the distinction between groups made artificially on a single criterion, and those made naturally — the Aristotelian "kinds". It is worth quoting in extenso:

> "It appears that the properties, on which we ground our classes, sometimes exhaust all that the class has in common, or contain it all by some mode of implication; but in other instances we make a selection of a few properties from among not only a great number, but a number inexhaustible by us, and to which as we know no bounds, they may, so far as were are concerned, be regarded as infinite.
>
> There is no impropriety in saying that of these two classifications, the one answers to a much more radical distinction in the things themselves, than the other does. And if any one even chooses to say that the one classification is made by nature, the other by us for our convenience, he will be right; provided he means no more than this, — that where a certain apparent difference between things (although perhaps in itself of little moment) answers to we know not what number of other differences, pervading not only their known properties but properties yet undiscovered, it is not optional but imperative to recognise this difference as the foundation of a specific distinction: while, on the contrary, differences that are merely finite and determinate, like those designated by the words white, black, or red, may be disregarded if the purpose for which the classification is made does not require attention to those particular properties. The differences, however, are made by nature, in both cases; while the recognition of those differences as grounds of classification and of naming, is, equally in both cases, the act of man: only in the one case, the ends of language and of classification would be subverted if no notice were taken of the difference, while in the other case, the necessity of taking notice of it depends upon the importance or unimportance of the particular qualities in which the difference happens to consist.
>
> Now, these classes, distinguished by unknown multitudes of properties, and not solely by a few determinate ones, are the only classes which, by the Aristotelian logicians, were considered as genera or species."

MILL, who had some familiarity with biological classification and [some experience of species in the field, was clearly impressed, as the vast majority of naturalists have always been, with the distinctness of "kinds" of organisms. Any philosophical account of biological classification, or for that matter any practical procedure, which does not, as it were, take this psychological fact into account, is unlikely to commend itself to the biologist of today any more than it would to Linnaeus. Yet the peculiar impact of Darwin's work on this problem was to deprive all taxonomic categories, family, genus and species alike, of "objective existence". Thus DARWIN himself wrote of the species: — "I look at the term species as one arbitrarily given for the sake of convenience to a set of individuals closely resembling each other." (Origin of Species, 1859), and in the writings of many scientists in the latter half of the nineteenth century we find similar ideas expressed. For example JEVONS (1877) in a general text-book "Principles of science" states: "We now, however, perceive that the existence of such groups as genera and species is an arbitrary creation of the naturalist's mind." It seems that in refuting the dogma of special creation Darwin and the Darwinians were over-zealous, perhaps understandably so. To dismiss the recognition of natural "kinds" as arbitrary creations of the naturalist's mind is perhaps permissible if done by the nominalist philosopher as part of a general philosophical assessment; but neither Darwin nor his followers in general were equipped to do this. Mill's analysis of the problem, for all its ignorance of the evolutionary proces, is nevertheless both more useful and more realistic.

Of course the important Darwinian contribution to the theory of natural classification was the explanation offered by the idea of common descent for the hitherto mysterious "affinities" between organisms and between classes of organisms. Whatever their views on more controversial questions, most biologists since Darwin have agreed that their ability to make any reasonably agreed natural classification of organisms depends upon the fact of organic evolution and the laws of inheritance. (It was inevitable that post-Darwinian writers interpreted the existing natural classifications naively in a phylogenetic sense; but a discussion of this aspect of the subject lies outside the scope of this paper.)

It is very significant that in practice it made no visible difference to taxonomic method whether the expert was working on an explicitly Aristotelian framework of "natural" genera and species (as Linnaeus), on a basis of "reality" of the species only (as de Candolle or Lindley) or on a basis of the Darwinian view that all taxonomic categories were convenient abstractions from a complex of populations varying in space and time. The practical importance of taxonomy, to provide a general framework of reference for the science of Botany as a whole, has ensured that the Linnean binomials and the system of classification of genera into families largely stabilised by de Jussieu have remained to the present day. Nor is it within the bounds of practical possibility to scrap the "classical" herbarium taxonomy for the Flowering Plants and substitute any fundamentally different method, even if it were clear on theoretical grounds that a different system would be more useful.

Experimental taxonomy

The twentieth century has seen the growth of understanding of the nature of variation and the laws of heredity, and the impact of modern cytogenetics on taxonomy raises practical questions which in themselves have stimulated theoretical discussions. The relevance to taxonomy of knowledge of the variability of populations has of course long been appreciated; but it is only within the last half-century that botanists have undertaken the large-scale experimental investigations which reveal the different patterns of genetical behaviour underlying the orthodox taxonomic patterns of morphological difference. Today this new body of knowledge is so important and extensive that in its taxonomic application it is generally distinguished from the "classical" or "orthodox" taxonomy as "biosystematics" or "experimental taxonomy". A valuable account of this new field of knowledge was provided by HESLOP-HARRISON (1953); and the relevant literature was admirably surveyed by STEBBINS (1950) in his detailed text-book "Variation and Evolution in Plants".

In the present paper, I shall confine myself rather rigidly to considering the relevance of biosystematic investigation to the definition and use of the categories of genus and species. It is here that disagreements arising from a desire to use new knowledge assume the greatest practical importance. It is a matter of indifference to the vast majority of botanists whether *Paeonia* should be included in the *Ranunculaceae* or dignified by being given a separate family; but no-one who uses the names can escape the consequences of splitting the genus *Lycopodium* or the species *Eleocharis palustris*.

In one important sense, the majority of biologists interested in classification since DARWIN have disagreed with something which DARWIN explicitly stated (see above); that is, they have reverted to the traditional view that the majority of taxonomic species are "real entities" which it is their business to "discover" in nature.* This common-sense view that there are "kinds" of organisms, which as we have seen was present in Aristotelian thought, is particularly obvious in the writings of zoologists; and it would be useful to consider why this should be so. From Greek times onwards, Man and the higher animals have naturally ranked very largely as examples in discussions on the logic and principles of classification. Thus the standard examples of Aristotelian logic used by MILL (1843) all concern "Man" as an "animal", and the three papers on classification by the eighteenth-century philosopher KANT consider the logical and philosophical implications of attempts to classify "the human race" (see RABEL 1927 pp. 269 et seq.). The peculiar importance of comparative zoology in the foundation of the theory and practice of "natural classification" was seen with particular clarity by the French philosopher Auguste COMTE, "the founder of Logical Positivism", whose writings on classification had particularly impressed MILL. COMTE writes (trans. MARTINEAU, H. 1853): "The multiplicity and complexity (of organisms), are not . . . obstacles to the systematic arrangement; on the contrary, they are aids, as the diversity of their relations offer a greater number of analogies . . . That is the reason why the classification of animals is superior to that of vegetables . . ."

It is not therefore surprising that the species-concept is greatly influenced by — indeed one might say based upon — the situation to be found in the *Mammalia*. Now *Homo sapiens* is an "ideal" species; that is, it is sharply demarcated morphologically from other living anthropoids, and so far as we know all races of man are inter-fertile. It is this coincidence of morphologically-defined "orthodox" species and genetically-defined interbreeding groups which has naturally and consistently attracted the attention of biologists. We find explicit references to it, for example, in the writings of RAY (1686); and it was easy to accommodate the dogma of special creation to such a dual criterion of the species. The inter-fertility of individuals of the same species, and their sterility with individuals of other species, fitted well with the notion that each species had in fact been created as distinct; the Adam and Eve legend for the origin of man served as a model for the whole of created life, and all existing members of any species were the descendants of an original pair. As GILMOUR has pointed out in a recent review of the species-concept (1958) there is no doubt that the idea of the species still comes to us "trailing clouds of special-creation glory"; and it was precisely this view of the "real species" which Darwin was at pains to refute.

The synthesis of Darwinian and Mendelian ideas in population genetics does, however, focus attention upon a unit of great evolutionary significance, namely the actual interbreeding population or gamodeme, defined as "an assemblage of individuals so situated in space and time and so similar to each other in morphology and physiology that they are all capable of interbreeding within the limits imposed by sex differences, incompatibility barriers, and the like". (HESLOP-HARRISON 1960; GILMOUR and HESLOP-HARRISON 1954**)). The relationship between a unit defined in this way and one defined on morphological criteria is both of theoretical and practical importance; theoretically because an understanding of small-scale or micro-

---

* See ČELAKOVSKÝ (1873) for an early qualified acceptance of "Darwinism" as applied to the species problem.

** All terms ending in the suffix "-deme" are defined in this paper.

evolutionary processes depends upon an adequate description, in genetical terms, of the process usually described in terms of the morphology of the individual phenotype as "speciation"; and in practice, because there is a natural tendency on the part of taxonomists to wish to employ in the definition of their taxa these important genetical criteria. Now it is on practical grounds, inherent in the nature of the experimental material, that the Angiosperm taxonomist (and indeed the botanist in general) finds himself unable usefully to "equate" the species of orthodox taxonomy, with an experimentally-defined "hologamodeme" ("genetical species", "ecospecies" of TURESSON). It is obvious to the flowering-plant taxonomist that the species which he describes and to which he gives binomials necessarily show when investigated biosystematicaly many different situations. This has been recognised and exemplified in the "Short Guide for Contributors to Flora Europaea" (HEYWOOD, (ed.) 1958), where the following statement was made by the Editorial Committee:

> "All available evidence . . . should be taken into consideration in delimiting species, but the species so recognised must be definable on morphology. The species, defined morphologically, will however illustrate different kinds of evolutionary situations; in other words, species are equivalent only by designation, and not by virtue of the nature or extent of their evolutionary differentiation."

It is in fact surprisingly difficult to find an example of an "ideal" or uncomplicated species amongst the rapidly-growing number of cases which have been investigated in flowering plants by modern bisystematic methods. Far from being the normal situation, a clearly morphologically-definable species of plant which is also a single hologamodeme looks almost like the exception. Of course, our sample of cases investigated is biassed, for there has naturally been a tendency to study situations where the evidence of orthodox taxonomy and field behaviour suggests that some complication is present; but the total amount of relevant data which we now have at our disposal for the European Flora would not encourage anyone to look for a general coincidence of genetically-defined populations with morphologically-defined species.

Apomixis

In considering the genetical phenomena shown by flowering-plant species, it is perhaps most useful to eliminate first the cases of non-sexual reproduction or apomixis. In the narrower sense of the term, as involving reproduction by seed but without fertilisation (agamospermy, c.f. GUSTAFSSON, 1946), this phenomenon is now known to characterise certain notoriously-difficult "critical groups" of species or whole genera. It is indeed one of the obvious triumphs of cytogenetic study that apomixis and its relationship to taxonomic complexity is now so well understood, although much more in detail remains obscure in each particular case. A peculiar difficulty of discussing the taxonomic treatment of apomicts is that a whole range of genetical and taxonomic situations is involved, and a solution which is practicable in one case may well prove unworkable in another. In one general respect, however, the taxonomic problem of the major apomictic groups is easy . . . namely in that there is very general agreement amongst taxonomists that any treatment adopted is necessarily incomplete and is to be judged in simple terms of its convenience and utility. Apomictic species to which binomials are given are so obviously undefinable on any criteria other than the traditional ones of morphology that the only remaining possibility of argument is whether a detailed classification of many "micro-species" serves any useful purpose. It is impracticable to consider in any detail more than one or two selected cases of apomictic groups in the European flora, and I shall therefore confine my remarks very largely to the genus *Alchemilla* and the *Ranunculus auricomus-cassubicus* complex, as examples differing both in genetical nature and in terms of possible taxonomic treatment.

In the case of *Alchemilla*, an orthodox taxonomy, in which a large number of species were described within the Linnean *A. vulgaris* and *A. alpina*, was provided in the latter part of the nineteenth century by the Swiss botanist BUSER. The taxa described by Buser and earlier taxonomists ranged from widespread European species such as *A. monticola* OPIZ (*A. pastoralis* BUSER) to very local endemics such an *A. faeroensis* BUSER of Iceland and the Faeroes. They are mostly "good" species in the traditional taxonomic sense; that is, a key can be made to enable the student to identify well-grown material with considerable success, and they possess characteristic geographical distributions, and in some cases distinct ecological preferences. There can be little doubt that, had only a few such species occurred in Europe, they would have been in no way "critical" . . . and indeed this is the case in regions where *Alchemillas* as a whole are rare, for example, in Ireland, where the six species which occur can be distinguished very easily.

The cytogenetic investigation of *Alchemilla* dates back to the very early days of such work, and is associated with the names of Strasburger and Murbeck in the last years of the nineteenth century. We now know that all investigated *Alchemillas* of the "*vulgaris*" group (Section *Heliodrosium* ROTHM.) and nearly all of the "*alpina*" group (Section *Chirophyllum* ROTHM.) are totally apomictic, with wholly or largely degenerate pollen and agamospermous seed. Only the morphologically isolated Linnean species *A. pentaphylla* and a very few "*alpina*" species are sexual. The orthodox taxonomy, so well executed by BUSER, has been extended by LINDBERG, SAMUELSSON, ROTHMALER, PAWLOWSKI and JUZEPČUK, until an adequate account of the *Alchemillas* of Europe is quite a practicable undertaking which Professor Rothmaler hopes to complete in the near future. Convenient bibliographies of the relevant literature are contained in ROTHMALER and JANCHEN (1957) and POELT (1958). For the purposes of Flora Europaea, I have suggested a possible abridged account which would describe all wide-ranging micro-species but omit some at least of the very local endemics (WALTERS in HEYWOOD 1960).

There is no serious practical difficulty in employing binomials and therefore treating as species the two or three hundred *Alchemillas* of Europe, for as we have seen earlier we are apparently prepared to tolerate genera with more than 2,000 species (*Senecio*) which are not known to be characterised by any reproductive peculiarity. The naming of many apomictic micro-species does, however, inevitably lead to the employment of binomials also as aggregate names; for the ecologist, often working with inadequate material in the field, it is important to have available the binomial "*Alchemilla vulgaris*" in the collective or aggregate sense, and the alternative "*Alchemilla* Section *Heliodrosium*" is too cumbersome to commend itself. The success of the binomial convention for apomictic groups is evident from a glance at the various accounts of *Alchemilla* in different Floras; these have achieved a degree of co-ordination which has not yet been possible in many less critical genera. JUZEPČUK stated (1958) "Systematists working with such genera have long been of the unanimous opinion that only a binomial system of nomenclature applied to every apomictic form is the rational method of research". With these sentiments I would agree, although I would attribute the unanimity of systematists working with *Alchemilla* to their realisation of the convenience of using binomials in the traditional manner, not to any "rationality" in the method of research.

The taxonomy of the *Ranunculus auricomus-cassubicus* complex, in which pseudogamous agamospermy is the rule, present a very different picture from that of *Alchemilla*. In this case there is no satisfactory nineteenth-century foundation for a detailed treatment, and instead we have as yet only fragmentary studies usually on a national or regional basis. Convenient bibliographies are given in JASIEWICZ 1956 and ROUSI 1956. It is quite impossible, in the present state of our knowledge of the group, to offer any reasonable account of the micro-species in Europe; and in the opinion of some at least of those who have specially studied this group, the very local endemism of most of the apomicts makes it unlikely that the pattern of variation over a wide area will be susceptible of the kind of taxonomic treatment which it has proved possible to apply to *Alchemilla*. It may well be that BUSER was not only particularly gifted in his ability to recognise and describe small but constantly-correlated differences as a basis for his species of *Alchemilla*, but he was also particularly fortunate in that the main patterns of variation so described are significant throughout the whole range of the group. If he had submitted *Ranunculus auricomus* to a similar treatment, it would apparently have been far less successful.

This kind of difference in pattern of variation between apomictic groups cannot yet be understood in terms of the probable evolutionary history; but it is tempting to suppose that the wide-ranging *Alchemilla* micro-species, showing within themselves considerable genetic variation (see TURESSON 1943), are old taxa, whilst local endemism in apomictic groups is likely to be indicative of more recent phenomena. The case of *Hieracium* is particularly interesting in this connexion, for among the many described apomictic micro-species in any one region (cf. PUGSLEY 1948 for the 260 species of the British Isles) there are wide-ranging species, sometimes with markedly disjunct distributions, and narrow endemics probably of recent origin.

The cases of apomixis so far mentioned are relatively simple, in that the majority of taxa described in each case are obligatorily apomictic. Genera such as *Poa*, *Calamagrostis* and *Potentilla*, however, in which partial or facultative apomixis occurs, present patterns of variation which no amount of careful study by the orthodox methods will resolve into definable species. The taxonomically recognisable species here may be, from a biosystematic point of view, highly complex groups consisting of several cytodemes ("chromosome races") each of which may be partially or wholly apomictic. This is obviously the case in the *Potentilla verna* aggregate in Europe (cf. SKALINSKA & CZAPIK 1958 and references given there). To what extent the known complexity of the species so distinguished should be further recognised by the use of infra-specific categories is a question which really lies outside the scope of this paper, but I shall refer briefly to the general problem later.

Autogamy

Another kind of reproductive situation which is found to underlie some cases of critical taxonomy is autogamy or habitual self-pollination. In such cases local populations tend to be largely homozygous and therefore relatively uniform in morphology, whilst being more or less sharply demarcated from adjacent populations. This type of variation is familiar in certain autogamous ephemeral weeds such as *Capsella bursa-pastoris*, and it is significant that all attempts to fit the undoubtedly large variation of *Capsella* into an orthodox taxonomic framework have proved unsuccessful. The classical case of *Erophila verna*, in which Jordan distinguished more than 200 "species", presumably owes its taxonomic intractability in part to autogamous reproduction, although as WINGE (1940) showed, polyploidy is also involved in this case. An interesting case recently described in some detail where autogramy is associated with taxonomic complexity and local speciation is that in the orchid genus *Epipactis*, where a group of taxa may be distinguished in which the flower-structure is secondarily simplified and self-pollination is obligatory (YOUNG, 1953).

Polyploidy

By far the most important micro-evolutionary situation with taxonomic implications is the phenomenon of polyploidy. The literature on this subject, is, of course, very large (cf. STEBBINS 1950 for the most important references) and I shall not attempt here to give any survey, but be content with some generalisations which can reasonably be made from the known facts, and the mention of one or two particular cases.

Firstly, it is clear that allopolyploid species-pairs or species-groups make up a considerable part of the European flora; many of the commonest species of Europe such as *Poa annua* L., *Dactylis glomerata* L., *Lotus corniculatus* L. are almost certainly of allopolyploid hybrid origin from diploid parent species, and there are few genera of reasonable size in the European flora in which some indication of polyploidy is not evident in the known chromosome numbers of the species.

Secondly, diploid-polyploid relationships may be accompanied by any degree of morphological distinction, from an obvious one which has provided the basis for a recognition of distinct species in the classical taxonomy (as in the case of *Viola reichenbachiana* JORD. ex BOR. and *V. riviniana* RCHB.) to one in which it is not possible even to make a statistical separation of the two cytodemes on mean cell size (as in the case of *Kohlrauschia* described by BØCHER 1953).The commonest situation, well illustrated by *Poa annua* (cf. TUTIN 1957), is one in which orthodox taxonomy had recognised the morphological differences correlated with the polyploidy at the level of variety, or if at specific level, the majority of taxonomists had not used the taxa so recognised. Thus the Northern *Poa supina* SCHRAD. and the W. Mediterranean-Atlantic *P. infirma* KUNTH which are almost certainly the parent species of the variable allotetraploid *Poa annua* L., had received relatively little taxonomic recognition until the cytological and micro-evolutionary situation was clarified. Many other examples of taxonomic "recognition" of polyploidy are given by LØVE (1951).

A third generalisation concerns basic chromosome numbers. A comparison of chromosome numbers in certain groups suggests that allopolyploidy was involved in the more distant evolution of many Angiosperms. Peculiar basic numbers characteristic of a sub-genus, genus or sub-family may have as their most plausible explanation an ancient allopolyploid origin (or origins) for the whole group. Thus in the *Gentianaceae* "the generic diversification . . . has been based on a high degree of alloploidy" (LØVE, D. 1953), and the whole sub-family *Pomoideae* of the *Rosaceae* have the basic number 17, plausibly related to other Rosaceous basic numbers $X = 8$ and $X = 9$. DARLINGTON (1956) should be consulted for other examples of this kind.

Polyploidy is therefore a widespread phenomenon responsible for so-called "abrupt speciation" and probably involved in earlier stages of Angiosperm evolution also. How far should knowledge of patterns of cytological relationship, or knowledge of micro-evolutionary polyploid situations, influence the orthodox taxonomy? It is at this point that there has been in recent years the largest measure of practical disagreement. Some have claimed (cf. VALENTINE and LØVE 1958, p. 160) "that the members of a polyploid series should generally be given specific rank, even when the morphological differences are very slight". The justification for this demand is usually that wherever possible the species of the taxonomist should be made to coincide with the hologamodeme of the biosystematist; and the reason for making such a demand has already been discussed. There is no doubt that, whether the taxonomist accepts or rejects the "genetical species" argument, he is likely to be swayed in his judgment of the rank to be assigned to a particular taxon if he finds that a definable morphological difference is correlated with a cytological one. In other words, in cases where the morphological distinctions are barely sufficient to provide a basis for specific difference, chromosome number provides, as it were, an additional taxonomic character. The diploid-tetraploid pair *Cardamine hirsuta* L. and *C. flexuosa* WITH. provide a good example. Most European Floras accept these two species; yet in practice their discrimination not infrequently presents difficulty, which we are apparently prepared to tolerate.

The use of cytological data at generic level also raises issues of practical importance. There is an increasing tendency to re-define genera by introducing new criteria, among them cytological information. The stated aim of some taxonomists is to produce "phylogenetically significant" genera, possessing, for example, the same basic chromosome number, and therefore assumed to have a common origin. Thus there is a great temptation to re-classify the *Primulaceae*, raising some of the Sections of *Primula* to the status of independent genera and demoting some of the existing genera; such a re-classification could reveal correlations between morphological resemblance and basic chromosome number which are not so obvious on a cursory inspection of the information as it is usually presented. Whether we do this or not should depend entirely on our assessment of the advantages (of pointing to such correlations) as against the disadvantages (of the nomenclatural chaos which would ensue). It is always important to ask whether an existing sectional classification of a genus could not (as in DARLINGTON and WYLIE 1955, pp. 276—8) reveal the correlations adequately enough for the purposes of experimental taxonomists and others interested in patterns of variation and evolution of the family. It is interesting that BABCOCK (1947) has not felt impelled to express the interesting correlation between basic number and sectional taxonomy in *Crepis* in a framework which departs significantly from the "orthodox" one.

Finally, the difficulty of partial or regional solutions must be mentioned. The case of *Valeriana officinalis* L. is a particularly interesting one. This widespread European species has been investigated both experimentally and by orthodox taxonomic methods in several parts of Europe by many different workers. A general picture emerges which is familiar enough; there are diploid, tepraploid and octoploid cytodemes which can to some extent be recognised by their morphology and ecological preference, and have significant geographical distributions. SKALINSKA (1951) states that the recognition of taxa corresponding in part to the cytodemes is easier in Poland than in some other parts of Europe, such as Britain, in which most populations consist of variable octoploids. A workable taxonomy for Poland would not necessarily be applicable to the same group in Western Europe, and there is a natural tendency to seek a taxonomic framework which will apply, so far as is known, throughout the area of the group concerned. In such cases, a provisional regional treatment, accompanied by a clear statement about the complexities of the problem, is obviously the only solution.

Hybridisation

It seems certain that the importance of hybridisation in the understanding of micro-evolutionary phenomena has been under-estimated in the past. Of course a number of spectacular cases of species-hybridisation have long been familiar in the European floristic literature (e.g. the fertile *Geum urbanum* × *G. rivale* hybrids, cf. MARSDEN—JONES 1930); but the existence of relatively few striking examples of this kind has probably tended to obscure rather than illuminate the more widespread subtle phenomenon to which ANDERSON (1949) first drew general attention — namely the "introgressive hybridisation" or restricted gene-flow from one species into a related one incompletely separated by genetical and/or geographic-ecological barriers. BAKER (1951) has produced a very valuable general review of the possible importance of this kind of phenomenon.

Realisation of the widespread nature of hybrid phenomena, particularly in a flora such as that of Northern and Central Europe which has been profoundly and recently affected by glaciation, must naturally have its effect on taxonomy, and indeed we have already discussed the particular phenomenon of allopolyploid hybridisation. In certain extreme cases (such as that of the genus *Salix*, investigated experimentally by NILSSON 1930), it seems that the extent of hybridisation, coupled with effective vegetative propagation, has produced a pattern of variation in which the delimitation of taxonomic species must be more than usually arbitrary. In such cases disagreements about the nature and delimitation of taxa are inevitable, and the ordinary taxonomist must be provided, if necessary, as in the apomictic groups, with aggregate or sectional names for general use. Thus the majority of British botanists find a distinction at specific level between *Salix cinerea* L. and *S. atrocinerea* BROT. more or less unworkable, although in the Atlantic parts of Continental Europe the two taxa are apparently more effectively distinct. A similar case is provided by the two *Betula* spp., *B. pendula* ROTH. and *B. pubescens* EHRH. In parts of Europe (e.g. Finland) there is little difficulty in naming trees in the field, and the taxonomic differences are paralleled by different ecological preferences; but in areas such as lowland England where most *Betula* woodland has a highly complex history, fertile hybrid populations are common, and individual trees cannot be assigned to one or other species.

Many more subtle cases of introgression will undoubtedly be described in the European literature; a recent one of some interest is that in *Euphrasia*, investigated by YEO (1955). Here there is good evidence of introgression from tetraploid to diploid species, and at least one local taxon which has been given specific rank (*E. vigursii* DAVEY) seems likely to have originated in this way.

In any such case the framework of orthodox taxonomy is likely to be affected by the experimental evidence. One general problem which emerges is that of deciding what degree of introgression need be demonstrated before a species is to be formally designated "hybrid". This is, of course, another aspect of the problem of the variability of species, to which we must now turn.

Variability of sexual species

Recognition of important genetic variation within and between local populations of ordinary sexual species has led to considerable discussion as to how, if at all, such knowledge is to be accommodated into the "legally permissible" framework of "subspecies", "varietas" and "forma" provided by the International Code of Botanical Nomenclature. Widespread ecotypic and regional variation patterns are normally exhibited by common European species, and to some extent these patterns have already received recognition in the detailed orthodox taxonomy. Thus in the case of *Silene vulgaris* L. sens. lat. investigated by MARSDEN—JONES and TURRILL (1958), names are available (some at specific level) for five of the six taxa which they recognise as subspecies with geographical differentiation in Europe; and in the very complicated case of *Campanula rotundifolia* L. (BØCHER 1960) a few of the diploid cytodemes (2n = 34) correspond with described taxa, though the majority of species described within the aggregate contain both diploid and tetraploid plants.

The taxonomic treatment of ecotypic and other local genetically-based variation lies outside the scope of this paper, but the recognition of geographical variation patterns is relevant, because in practice taxonomists usually have to choose between specific and subspecific rank for such cases. A comparison of treatment in some of principal Floras of Europe shows great differences in this respect, ranging from a complete absence of subspecies in KOMAROV (1934) to a considerable use in HEGI (1906). This lack of uniformity causes nomenclatural complications, and naturally makes the use of the literature in the preparation of Flora Europaea even more difficult than it might otherwise be. JUZEPČUK's defence of the KOMAROV concept of the species (1958) — which amounts to a justification of the ban on the use of the subspecific category — is interesting, not least for its historical survey of the species concept in the Russian botanical literature. It is, however, difficult to see either the theoretical necessity or the practical advantage of using the binomial so widely for taxa in which the morphological differences are inadequate for determination by the standards of taxonomic practice. The effect is often to make the Komarov "series" an aggregate, or species *sens. lat.* The same kind of information is being conveyed, whether the subspecies is used or not, and the decision as to whether in any particular case it should be used ought reasonably to be based upon the practicability of identifying a specimen. If the morphological and anatomical differences are either so incomplete or so difficult that a significant number of specimens (say more than 10%) cannot be assigned with reasonable certainty to the taxon concerned, then it will be inconvenient to designate it by a binomial. JUZEPČUK says (1958) that "we must strive to represent nature as it is, and not as it would suit us or simply as we should like it to be", implying that there is only one "kind" or grouping in Nature whose recognition is, as it were, scientifically respectable . . . and that "kind" must in every case receive a binomial and ipso facto be a species.

JUZEPČUK's claim, to recognise species as "kinds" in nature, is therefore in the long tradition of biologists impressed with the facts of morphological discontinuity and the more or less satisfactory correlations with geographical distribution, ecological preferences or genetical criteria. (cf. for example DU RIETZ 1930 & ROTHMALER 1944). His adverse criticism of VAN STEENIS (1957) — though admittedly the work was available to him only after he had completed the article — seems a little odd, in that Van Steenis' general species concept is, like that of Juzepčuk, based on the recognition of morphologically different "kinds" in the field. In two respects, however, Van Steenis' recommendations conflict with those of Juzepčuk; firstly he advocated a wide species concept; and secondly he is impressed with the genetic species criterion, arguing, for example, that in view of the "miscibility" of *Geum urbanum* L. and *G. rivale* L. it is "scientifically erroneous and educationally reprehensible" to continue to distinguish them as species.* VAN STEENIS is nevertheless (in company with most taxonomists and field botanists) cautious in that he effectively subordinates any genetical criterion to a morphological one. His paper contains an immensely valuable bibliography of all aspects of the subject of modern Angiosperm taxonomy.

It seems to be true that nearly all the writers on the species concept assume that a particular "real entity" or "kind" is discoverable in any and every case, and that the business of the investigator is to discover and describe it, and if he is a taxonomist, to name and classify it. Those to whom some kind of genetical criterion is of paramount importance will find that kind of "real" species; and they will argue with those who claim that the "population in nature" or "the group of individuals possessing certain hereditary characters" is the "kind" they are looking for. The arguments become heated precisely because the "kinds" differently defined will not always coincide. Of course they may and often do coincide, and a study of the significance of this is of profound importance for the understanding of the micro-evolutionary process; but we must not complain if they do not.

Conclusion

The dilemma evident here is the general one which we have exemplified earlier, and which applies to generic as well as to specific delimitation. It may be stated in the form of a double question: firstly, "can we satisfactorily define and name units which will form a basis for a hierarchical classification?" and secondly "should our aim be to perfect a single "natural" classification which can embody all kinds of information in the definition of its constituent taxa?"

The first question is obviously already answered so far as the vascular plants are concerned; we are operating reasonably effectively with a classification which has been traditionally shaped. Yet it is worth remembering that

---

* GAJEWSKI (1951) has pointed out the chaotic implications of Van Steenis' argument in the genus *Geum*; at the conclusion of one of the most detailed systematic studies of any European genus he states:

"The overwhelming majority of species from the subgenus *Eugeum* cross among themselves quite easily, and almost the whole of the subgenus could be included in one coenospecies. Some species . . . in Clausen's system of classification . . . could be even included in one ecospecies . . . The conclusion which is to be drawn from these considerations is that incompatibility barriers often depend on factors which are not distributed within a genus in a manner strictly correlated with the degree of morphological differentiation between species."

there are groups of organisms for which a clear answer to this first question has not yet been given — for example, the Bacteria (cf. LYSENKO and SNEATH 1959). It is also important to remember that we are using a classification which, as we have seen, bears very obvious marks of its history upon it; this necessarily means that if we could "wipe the slate clean" and start again, we should not expect to get the same result. The absence of an agreed method of procedure and of an agreed philosophical basis would in fact prevent us from starting again, even if we wished to. It is possible, for example, that we would wish to decide whether our classification should be "typological", forming its groups by reference to, or association around, a type specimen or type concept, or whether it should proceed in some other way which many would think was more "respectable" scientifically. The philosophical implications of typology in biology are still disputed and likely to remain so for some time (cf. for example ZIMMERMANN (1959)). A discussion of the typological basis of a "natural" classification is not possible here, but it leads us directly into the second question — is a single perfect classification our aim?

The attraction of the idea of what TURRILL (1942) has called an "omega-taxonomy" is obvious enough. It is a comforting thought that we could continue to "improve" our existing morphologically-based classifications by employing more and more criteria derived from new techniques or called forth by new kinds of investigation. Even if the process is painful — as when some traditionally-hallowed piece of classification has to be abandoned — is not this inevitable in the name of scientific progress? Belief in an "ideal" classification which would somehow serve all purposes and contain all knowledge is a very strong factor, consciously or subconsciously, in the mind of most taxonomists, and in so far as it is rationally expressed, it tends to be presented in a phylogenetic (evolutionary) guise. The argument runs thus: we must assume that evolution has taken a particular course; all taxa can therefore be thought of as related to all other taxa in a particular way and to a particular degree; it is therefore theoretically possible so to order our classification that it reflects accurately the course of evolution.

But is not this an impossibly naive view? Why should a two-dimensional hierarchical classification be able to express all the complexities of evolution? It is obvious enough, for example, from what little we know of allopolyploid micro-evolution, that polytopic origin and reticulation can occur, and may occur frequently; and no amount of juggling with the boundaries of taxa can hope to express a fraction of this possible evolutionary complexity alone. Ignoring, then, any theoretical or philosophical considerations, the yearning for an "omega-taxonomy" seems on practical grounds to lead to frustration and disappointment.

There are, however, serious philosophical objections to the search for an "ideal" or "omega-taxonomy", inherent in the nature of the activity of classification itself. These objections could be briefly summarised as follows. The "rightness" or "wrongness" of any piece of classification — or indeed of any statement at all — is to be judged by reference both to the "objective facts of nature" and to the purpose for which the classification is made (or the context in which the statement is made). In practice most scientists do proceed in their enquiries in this way, insofar as they are conscious of adopting a particular mental procedure. Certain types of scientific argument, however, arise inadvertently because this procedure is not in fact being followed.

A "natural" clasification is somehow conceived of as being ultimately "right" — either for all purposes, or for an undefined purpose — whilst "mere" artificial classifications are conceded as "useful" or "right" for particular purposes. The general statement of the view of language here implied is due to CRAWSHAY—WILLIAMS (1957).

Adopting this method of enquiry, the legitimate question then would seem to be this: if we make (or use) "natural" classifications based on maximum correlation of attributes, and which therefore recognise objectively definable discontinuities of various kinds, for what purposes are these classifications useful? Much recent discussion on the theme has centred around the mathematical approach to the problem of making "natural" classifications, and there is a danger that the biologist may be substituting a new "ideal" or "omega-taxonomy", namely that which the mathematician can produce for him, which he would feel justified itself and did not require reference to a purpose. (SNEATH (1958) discusses some of these questions and gives a useful bibliography.) It seems important for the taxonomist, in this situation, to make a strong plea for the continued recognition of an "orthodox" morphologically-based taxonomy as providing a general-purpose classification, and permitting a wide range of valuable generalisations to be made. In particular he must resist pressure from all specialists to alter radically this framework to suit either their particular concern (evolutionary relationship, genetic similarity, "biological significance") or the demands of an undefinable "omega-taxonomy". He should insist that they use special terminology and where necessary special classifications to express their particular interest. In so doing he will be serving the interests of the science as a whole, to which a workable general reference system is just as necessary today as it was in the time of Linnaeus.

Summary

The paper gives a brief historical survey of the concepts of genus and species in the European flora, and considers in particular their origin in Aristotelian logic. It stresses that the main framework and the procedures of Angiosperm taxonomy are pre-Darwinian, and considers the impact of Darwin's ideas, those of his contemporaries and successors, and the "experimental taxonomy" of the present century on this traditional discipline. Some indication is given of the main types of micro-evolutionary situation in flowering plants, with examples from recent literature. The suggestion is made that arguments about the reality of "kinds" in nature, as also the desire for a single "omega-taxonomy", both arise from an inadequate philosophical view of the nature and purpose of classification. The final recommendation is that the traditional morphologically-based taxonomy must be retained for the general reference system of the science as a whole, and that special studies must, as and when necessary, operate with separate specialised terminologies.

References

ANDERSON E. (1949): Introgressive Hybridization. New York.

ARBER A. (1938): Herbals, ed. 2. Cambridge.

BABCOCK E. B. (1947): The Genus Crepis. Univ. California Publ. Bot. **21**.

BAKER H. G. (1951): Hybridisation and Natural Gene-Flow between higher plants. Biol. Rev. **26**, 302.

BAUHIN G. (1623): Pinax Theatri Botanici. Basle.

BØCHER T. W. (1953): Experimental and Cytological Studies on Plant Species. I. *Kohlrauschia prolifera* and *Plantago coronopus*. Hereditas **39**, 289.

BØCHER T. W. (1960): Experimental and Cytological Studies on Plant Species. V. The *Campanula rotundifolia* complex. Biol. Skr. Dan. Vid. Selsk. **11**, no. 4.

CAIN A. J. (1958): Logic and Memory in Linnaeus' System of Taxonomy. Proc. Linn. Soc. Lond. **169**, 144.

Candolle A. P. de (1813; ed. 2. 1819): Théorie Élémentaire de la Botanique. Paris.

Čelakovský L. (1873): Über den Begriff der Art in der Naturgeschichte, insbesondere in der Botanik. Oest. Bot. Zeitschr. **23**, 233, 271, 313.

Comte A. trans. Martineau H. (1853): Positive Philosophy. London.

Crawshay-Williams R. (1957): Methods and Criteria of Reasoning. London.

Darlington C. D. (1956): Chromosome Botany. London.

Darlington C. D. and Wylie A. P. (1955): Chromosome Atlas of Flowering Plants. London.

Darwin C. (1859): Origin of Species. London.

Du Rietz G. E. (1930): The Fundamental Units of Biological Taxonomy. Svensk. Bot. Tidskr. **24**, 333.

Gajewski W. (1957): A Cytogenetic Study of the Genus *Geum*. Monographiae Botanicae, Warschawa, **4**.

Gilmour J. S. L. (1958): The Species: Yesterday and Tomorrow. Nature, **181**, 379.

Gilmour J. S. L. and Heslop-Harrison J. (1954): The deme terminology and the units of microevolutionary change. Genetica. **27**, 147.

Gustafsson Å. (1946): Apomixis in Higher Plants. Lunds Univ. Årsskr. N. F. 2, **42**.

Hegi G. (1906—): Illustrierte Flora von Mittel-Europa. München.

Heslop-Harrison J. (1953): New Concepts in Flowering-Plant Taxonomy. London.

Heslop-Harrison J. (1960): Infraspecific Differentiation. Planta Medica, (Stuttgart) **8**, 208.

Heywood V. H. (ed.) (1958): The Presentation of Taxonomic Information — A Short Guide for Contributors to Flora Europaea. Leicester.

Heywood V. H. (ed.) (1960): Problems of Taxonomy and Distribution in the European Flora. Feddes Repert. **63** : 111—228.

Jasiewicz A. (1956): De Ranunculis e circulo *Auricomi* Owcz . . . Fragmenta Flor. et. Geobot., Krakow, **2**, 62.

Jevons W. S. (1877): Principles of Science. ed. 2. London.

Jussieu A. L. de (1789): Genera Plantarum. Paris.

Juzepčuk S. V. (1958): The Komarov concept of the species, its historical development and expression in the "Flora U.S.S.R." "The Species Problems in Botany" (Moscow—Leningrad) **1**, 130.

Юзепчук, С. В. (1958): Комаровская концепция вида, ее историческое развитие и отражение во флоре СССР. Проблема вида в ботанике (Москва-Ленинград) **1**, 130.

Komarov V. L. (ed.) (1934—): Flora S.S.S.R. Leningrad.

Комаров, В. Л. (1934—): Флора СССР. Ленинград.

Linnaeus C. (1751): Philosophia Botanica. Stockholm.

Linnaeus C. (1753): Species Plantarum. Stockholm.

Løve A. (1951): Taxonomical Evaluation of Polyploids. Caryologica (Pisa) **3**, 263.

Løve D. (1953): Cytotaxonomical Remarks on the *Gentianaceae*. Hereditas **39**, 225.

Lysenko O. and Sneath P. H. A. (1959): The Use of Models in Bacterial Classification. Journ. Gen. Microbiol. **20**, 284.

Marsden-Jones E. M. (1930): The Genetics of *Geum intermedium* Willd . . . Journ. Gen. **23**, 377.

Marsden-Jones E. M. and Turrill W. B. (1958): The Bladder Campions. London.

Mill J. S. (1843): System of Logic. London.

Morison R. (1672): Plantarum Umbelliferarum Distributio Nova. Oxford.

Nilsson N. H. (1930): Synthetische Bastardieringsversuche in der Gattung *Salix*. Lunds. Univ. Årsskr. N. F. 2, **27**.

Poelt J. (1958): Die Gattung *Alchemilla* in Südbayern ausserhalb der Alpen. Ber. Bayer. Bot. Ges. **32**, 97.

Pugsley H. W. (1948): Prodromus of the British *Hieracia*. Journ. Linn. Soc. Lond. (Botany) **54**.

Rabel G. (1927): Goethe und Kant. Wien.

Ray T. (1686): Historia Plantarum, vol. 1. London.

Rothmaler W. (1944): Systematische Einheiten in der Botanik. Feddes Repert. **54**, 1.

Rothmaler W. and Janchen E. in Janchen E. (1957): Die *Alchemilla*-Sippen Österreichs in Catalogus Florae Austriae. Wien.

Rousi A. (1956): Cytotaxonomy and Reproduction in the Apomictic *Ranunculus auricomus* group. Act. Bot. Soc. "Vanamo", **29**, No. 2.

Scheuchzer J. (1719): Agrostographia. Zürich.

Skalinska M. (1951): Studies in Cyto-ecology, geographic distribution and evolution of *Valeriana* L. Bull. Acad. Polon. Sci. et Lett. Sér. B. **1**, 1950.

Skalinska M. and Czapik R. (1958): Studies in the Cytology of the Genus *Potentilla* L. Acta Biol. Cracov. Sér. Bot. **1**, 137.

Sneath, P. H. A. (1958): Some aspects of Adansonian classification and of the taxonomic theory of correlated features. Annali di Microbiologia ed Enzymologia, **8**, 261.

STEARN W. T. (ed.) (1957, 1959): LINNAEUS: Species Plantarum 1753. Fascimile. 2 Vols. London.

STEARN W. T. (1959a): Botanical Exploration to the Time of Linnaeus. Proc. Linn. Soc. Lond. **169**, 173.

STEBBINS G. L. (1950): Variation and Evolution in Plants. New York and London.

TOURNEFORT J. P. de (1700): Institutiones Rei Herbariae, ed. 2. Paris.

TURESSON G. (1943): Variation in the Apomictic Micro-species of *Alchemilla vulgaris* L. Bot. Notiser **1943**, 413.

TURRILL W. B. (1942): Taxonomy and Phylogeny. Bot. Rev. **8**, 247, 473, 655.

TUTIN T. G. (1957): A Contribution to the Experimental Taxonomy of *Poa annua* L. Watsonia **4**, 1.

VALENTINE D. H. and LØVE, A. (1958): Taxonomic and Biosystematic Categories. Brittonia **10**, 153.

VAN STEENIS C.G.G.J. (1957): Specific and Infraspecific Delimitation. Flora Malesiana ser. 1, **5**, 167.

WALTERS S. M. (1961): The Shaping of Angiosperm Taxonomy. New Phytologist **60**, 74.

WILLIS J. C. (1949): Birth and Spread of Plants. Geneva.

WINGE O. (1940): Taxonomic and Evolutionary Studies in *Erophila* . . . Compt. Rend. Lab. Carlsberg. Sér. Phys. **23**, 17.

YEO P. F. (1955): Hybridisation between Diploid and Tetraploid Species of *Euphrasia*. Watsonia **3**, 253.

YOUNG D. P. (1953): Autogamous *Epipactis* in Scandinavia. Bot. Notiser **1953**, 253.

ZIMMERMANN W. (1959): Die Phylogenie der Pflanzen, ed. 2. Stuttgart.