THE MOVING STAIRCASE:
A DISCUSSION ON TAXONOMIC RANK AND AFFINITY

P. H. DAVIS

ABSTRACT. The principles and practice of Angiosperm classification are discussed and exemplified, emphasis being given to ordinal, familial, generic, specific and infra-specific levels. Particular attention is paid to the inter-relationship of rank and affinity, influence of size of group on taxonomic treatment, problems of identification posed by increasingly phenetic classification, and the necessity of keeping phylogenetic speculation out of the classificatory process; failure to do so has resulted in the confused state of ordinal and supra-ordinal classification. Crossability and geographical isolation are discussed in relation to the taxonomic treatment of species and their infra-specific variation; the evolutionary potential of local varieties and sporadic forms is considered. The purpose and practical aspects of classification are stressed, and the desirability of improving classification by starting with species as the building bricks, instead of working downwards from 'received' higher groups.

> *The most curious part of the thing was,*
> *that the trees and the other things round them*
> *never changed their places at all:*
> *however fast they went,*
> *they never seemed to pass anything.*
> *"I wonder if all the things move along with us?"*
> *thought poor puzzled Alice.*
>
> Lewis Carroll

INTRODUCTION

This paper discusses the purpose and general aims of the taxonomic hierarchy in the Angiosperms, its use and abuse in particular cases, and the inter-relations between rank, affinity and convenience. I would have preferred to treat the hierarchy from the top downwards (as it is used), or from the species upwards (as it should be constructed), but this one-way approach has proved impracticable. Due to the nature of the hierarchical staircase, its steps tend to be uneven and unstable. I have therefore had to do a certain amount of going up and down stairs.

The following paragraphs deal with some general considerations affecting Angiosperm classification.

To start with a definition of a term used in this paper: *phenetic classification* is one based on overall similarity, not on known or inferred phylogeny; the characters used may or may not be weighted. It is a one-level, maximum-attribute, 'natural' classification, with high predictive value, and the phenetic groups comprising it are usually overlapping.

Changes in classification usually come about in two directions: horizontal and vertical.

1. *Horizontal changes*. These involve no alteration in rank but result from a change in assumed relationships—e.g. the transfer of a species from one genus to another, or from one family to another. Such changes usually occur

as a result of new evidence of natural relationships (often obscured by previously undetected convergence), or by removing imbalance caused by previous *a priori* weighting. Changes of this type are therefore to be welcomed when soundly based. Phenetic classification is improved mainly by horizontal changes, since these can bring together plants which share the greatest number of character states and thus increase the classification's predictive value. On the debit side, it widens the rift between the processes of classification (nested group-making) and identification. The more phenetic the groups become, the more overlap there is likely to be between the characters distinguishing the groups. For convenient identification on a world basis, highly phenetic groups often have to be keyed out a considerable number of times, e.g. the genus *Astragalus*, or when separating the Saxifragaceae from the Rosaceae. The higher one goes in the hierarchy, the greater the overlap between the groups, and thereby the harder identification becomes. That is a cross we have to bear in pursuit of advantages provided by phenetic classification.

2. *Vertical changes*. These are not usually influenced by considerations of relationship, but have other more arbitrary, often less scientific causes. The most important of these is the history of the group, which often dates back to medieval times, as discussed by Walters (1961, 1963). Extensive exploration over more than two and a half centuries has had the effect of greatly increasing the number and size of the genera, particularly during the 19th century (an acceptable by-product of imperialism). The taxonomic hierarchy has enlarged to accommodate the known diversity, so that more ranks have become available between family, genus and species. Families have tended to multiply, both by the discovery of very distinct new genera and by the splitting up of the 94 Angiosperm families first formally described in de Jussieu's *Genera Plantarum* (1789). Large families have been divided into subfamilies or tribes, genera into subgenera or sections. The families themselves (261 of them) were first grouped into orders in the modern sense (as *nixus*, ending in *-ales*) by J. Lindley in *Nixus Plantarum* (1833)—a remarkably practical pamphlet. It has been a roughly historical progression, the ranks being most used in the order in which they were first formally adopted. The modern tendency is to assign a higher rank to groups that previously had a lower one (e.g. by raising sections to generic rank), and to add new supra-ordinal ranks—an inflationary policy that tends to weaken the important synthetic aspect of classification.

Most vertical changes do not alter relationships. *Consolida*, for instance, previously a section of *Delphinium*, is now usually accepted as a separate genus (Munz 1967), but is still most closely related to *Delphinium*. However, it differs from the latter in its gamopetalous corolla with a single spur (unique in Ranunculaceae) and single follicle. As it is quite as well distinguished as several other genera traditionally accepted in the family, and a better genus than *Ceratocephalus*, its generic status can be justified in terms of consistency (see p. 327).

3. *Interaction between horizontal and vertical changes*. The distinction between horizontal and vertical taxonomic changes is not always clear-cut. *Paeonia*, for instance, was originally treated as a genus of Ranunculaceae, and later as

the type genus of a monotypic family, Paeoniaceae, now usually placed in the supposedly distant order Dilleniales. Some families have been dismantled because, in the light of phytochemical or micro-characters, their affinities evidently lie elsewhere. *Buddleja* has been taken out of the Loganiaceae and is now often considered as a separate family closely allied to the Scrophulariaceae. The separation of the Buddlejaceae can be justified on the basis of morphology, its affinities supported by the number of herbivorous insects that feed upon *Buddleja* and members of Scrophulariaceae (Crowson 1970). This still leaves the Loganiaceae, however, as an apparently heterogeneous group that has been further dismantled (Hutchinson 1959; Takhtajan 1969).

4. *Conflict between phenetic classification and ease of identification.* The choice between a highly phenetic system, and one that does not lose sight of convenient retrieval, can prove an agonising one for taxonomists. Some numerical taxonomists (e.g. Williams 1967) have advocated solving this dilemma by 'suboptimal classification'—e.g. an 'optimal' phenetic classification adjusted to make it more convenient to use.* This seems to me the most acceptable approach, unless we are prepared totally to divorce classification from the process of identification. For example, *Lathraea* has been traditionally classified in the Orobanchaceae on account of its parietal placentation combined with fully parasitic habit (lacking chlorophyll). Detailed developmental studies have demonstrated that *Lathraea* is more closely related to the Scrophulariaceae tribe Rhinantheae than with the Orobanchaceae, and is currently often placed in the former family. *Lathraea* is, admittedly, a go-between, but there seems no convenient way of separating these two families on a world basis if *Lathraea* is included in the Scrophulariaceae—though the families can be artificially keyed out on a national (country) level. It would seem more helpful to most users of classification to leave *Lathraea* on the Orobanchaceae side of the fence, as Airy-Shaw did in the 7th edition of Willis's *Dictionary of Flowering Plants and Ferns* (1966).

5. *Consistency of treatment.* Consistency is an important aim in taxonomy but is more easily approached in monographs than in Floras of multiple authorship. However, there is more chance of achieving consistency within a family than above it. Bentham & Hooker's *Genera Plantarum* (1862–1883) is a model of consistency of treatment combined with accuracy of description. However, much of the authors' 'consistency' is more apparent than real; it is achieved by consistently taking *size* into account, i.e. by separating small genera and families by larger gaps than those they deemed necessary for the separation of larger ones. By adopting this procedure Bentham & Hooker avoided the recognition of an inconveniently large number of very small or monotypic groups.

The 19th century monographs of genera [of which De Candolle's *Prodromus* (1824–74) provides the largest corpus] set a pattern that has persisted to the present time, though often in a modified form. However, in the case of the larger Dicot genera the *Prodromus* has not been replaced. *Ranunculus*, *Astragalus*, *Solanum*, *Cousinia* and *Senecio* have never been monographed to species level since De Candolle's time, despite (or because of) exploration having greatly increased these genera's size and complexity.

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* It might be argued, however, that no classification can ever be optimal.

The monographing of large families/subfamilies to species level seems to have nearly petered out with the collapse of Engler's *Das Pflanzenreich* series after the destruction of the Berlin herbarium in 1943. Perhaps it is no longer a practical proposition to monograph very large families to species level—only to monograph large genera (or groups of genera) within a family. To monograph very large groups now, with the vast amount of herbarium material and other data available, together with the increasing burden of synonymy, would certainly require extensive (and expensive) team work. However, the present high tide of Flora writing will presumably recede, freeing effective taxonomic manpower. I cannot help feeling that some of the energy that now goes into creating supra-familial edifices and phylogenetic schemes would be more helpfully channelled into the production of more practical monographs and revisions. The monographing of small genera several times (as has been the case with *Cyclamen* and *Digitalis*) suggests that a sense of priorities is often lacking in present-day taxonomy.

When engaged on major floristic work there is not enough time to give to the intensive world-wide survey that monography requires. A monographer who 'splits' may set a bad example for many decades, since his classification or species concept tends to get perpetuated (willingly or not) by harassed Flora writers, resulting in the description of more new microspecies of questionable validity; this applies particularly to apomictic groups. Only another, better monograph can set the record straight in the light of currently available material. Raven's (1976) regional revisions of *Epilobium* provide an excellent (too rare) approach to a moderately large, widespread genus. He is one of the few monographers who has managed to follow his genus round the world, studying it in herbarium, field and laboratory.

6. *Character weighting*. The historical weighting of characters in classification, both at generic and family level, has been very gradually modified by the more extensive use of vegetative ones. As the genera of Linnaeus and his successors were distinguished mainly on the basis of the flower and fruit, vegetative characters often had to be relied on for the recognition of sections. Whether floral characters are older (more conservative) than vegetative ones will vary from group to group, and it is going to be extremely difficult (often impossible) to tell which is which. It is partly because of uncertainty about the value of characters that 'unit' characters have been favoured by numerical taxonomists concerned with phenetic classification.

7. *Convergence and the archetype*. All organs of the plant can be influenced by convergent evolution, but it is usually functionally correlated suites of characters that are most likely to be affected (e.g. those making up the flower, or the dispersal unit). The adaptation, however, is not always obvious, nor the direction of the trend (e.g. inflorescence type, or placentation). It is the widespread occurrence of convergence and parallelism in the Angiosperms (in both phytochemical and morphological characters) that makes the assessment of phylogenetic relationships such a forbidding, if not impossible, task. This is especially true above the species level, where crossability criteria and genome analysis are seldom applicable. It has been frequently pointed out (often in vain) that phylogenists of the present-day flora have confused the evolution of organs (phylesis) with the evolution of taxa

(phylogeny). The organs of plants often evolve at different rates and are therefore out of step—Takhtajan's heterobathmy. The concept of the archetype, in which all the primitive features found in present-day groups once occurred together in its ancestor, must usually be a figment of the imagination. It is unlikely that any such desirable Boojum existed. I agree with Sneath & Sokal (1973), who are very interested in numerical studies on cladistics, when they say: "Not only do we insist on the separation of phenetic from phylogenetic considerations in taxonomic procedure, but we also feel that only phenetic evidence can be used to establish a satisfactory classification".

In the following pages I shall discuss rank and affinity etc. at the following three broad levels: generic and familial level; supra-familial level; species level and below. At each of these levels classification rather uneasily changes gear, due to the emphasis put on the criteria used or the purpose to which the classification is put.

GENERIC AND FAMILIAL LEVELS

The larger the genus the larger the number of subgenera, sections, subsections etc. are usually needed to accommodate its species. Above the level of the species there are no, even arbitrary, definitions of the taxonomic categories (ranks) *per se*. They depend on the size of the group and the opinion of the taxonomist, although some general level of consistency is usually attempted, at least within related groups. The adaptive versatility of the taxonomic hierarchy is both its strength and its weakness. Responsibly used, it provides the framework for very useful stable classifications. Badly used, it results in inconvenient instability, both taxonomic and nomenclatural.

GENERIC LEVEL. Accepted genera vary very much in their amenability to supra-specific classification, no doubt partly as a result of their unknown evolutionary history (including age, amount of extinction, etc.). Sometimes one may be able to draw a reasonable inference as to whether a certain state is older or younger than another in a genus. The large genus *Rhododendron* has been traditionally divided into two major groups on indumentum type—lepidote and elepidote groups. This division has since been found to correlate with ptyxis (leaves in bud flat to supervolute in the lepidotes, revolute in the elepidotes) and to a lesser extent with crossability and phytochemical characters (see Philipson, 1970, for a table of morphological characters). The lepidote group is currently treated by Cullen & Chamberlain (1978) as a subgenus with 3 sections, and the more diverse elepidote groups as 4 subgenera. As most genera in the tribe Rhododendroideae are elepidote with revolute ptyxis, it seems likely that the lepidote condition is a derived state in *Rhododendron*. *Crocus* (centred in the E Mediterranean) has long been divided on the presence or absence of a basal spathe, and further divided into sections based on the nature of the corm tunic. It seems probable that the characteristic crocus flower, fruit at ground level, and leaf form may have preceded the diversification of the corm.

The examples just mentioned, however, are exceptional. Far more often large and medium-sized genera do not divide readily into natural and convenient subgenera or sections: there are often a few isolated species, or small isolated species-groups, and a mass of other species that are difficult to classify—or the whole genus may consist of the last. *Onosma* (Boraginaceae) has traditionally been divided into two subgenera or sections on hair type—a convenient division for identification, but one which (unlike the situation in *Rhododendron*) repeatedly cuts across natural relationships as assessed on the basis of several other characters. *Isatis* (Cruciferae) has usually been divided into several sections on fruit characters (shape, width and thickness of wing, etc.), but these divisions, though a helpful guide through the maze, are partly artificial and certainly poorly delimited. However, *Isatis* is only one of numerous genera which do not seem to have any meaningful sections, being apparently still in an active state of evolution. *Verbascum*, *Nepeta*, *Cousinia* and *Echinops* lack a formal supra-specific classification that is of much use as a retrieval system, let alone one that is moderately natural. In genera which apparently lack satisfactory sections, the series is a category that might be used more often for groups of closely allied (usually sexual) species. Komarovian Soviet taxonomists, however, have often used this rank in a strongly phylogenetic sense (Davis & Heywood 1963, p. 102).

In some genera there is a tendency for a very small number of subgenera to be dropped in favour of a much larger number of more natural sections (e.g. New World *Salvia*, Epling, 1939; *Silene*, Chowdhuri, 1957). Other genera, like *Prunus* and *Satureja*, are going through an inconvenient "will she, won't she" period. Some taxonomists cling to a broad view of these two genera (recognising a number of subgenera or sections), while others raise the subgenera/sections to genera. In the case of *Prunus* the second view has the disadvantage of needing the 'stone' before the segregate genera can be identified, thus making it more difficult to construct a practical key to the species of *Prunus* sensu lato. On the other hand, narrow generic limits bring the group into line with *Malus* and *Pyrus*, which are weakly delimited in SE Asia. In *Satureja* sensu lato the major groups (*Satureja* sensu stricto, *Calamintha*, *Micromeria*, *Acinos*, etc.) work well enough as genera in the Mediterranean, but may not do so on a world basis—as Briquet maintained when he revised the Labiatae for the *Pflanzenfamilien* 4, 3a (1895–97). When writing a country's Flora one naturally tends to adopt the generic limits usually accepted in that region, since so much of the floristic literature is tied up with them. However, in the long run the broader view may prevail, but only a thorough reassessment of the problem on a monographic basis can hope to settle the matter.

Many early, heavily weighted classifications persist because they are still useful and nothing better has replaced them. *Valerianella*, monographed by Krock (1864), provides a good example and one that is now being reassessed. Krock based his numerous sections mainly on characters of fruiting calyx and cypsela. Given fruiting material, the system works well enough for identification. However, recent studies by Ernet (1977) have revealed a remarkable diversity of previously neglected characters—e.g. corolla shape, bract shape and other vegetative features. These often cut across Krock's groups and may lead to a more natural sectional classification; they have the added advantage of allowing more species to be identified in flower.

In a very perceptive paper, Burtt (1964), taking *Astragalus* and *Oxytropis* as an example, points out that genera differing in a single character are thereby not necessarily unnatural. It is possible that *Oxytropis* diverged early on from *Astragalus* stock in its functional diagnostic character (a beaked keel-petal), and that the pairs of similar species (one *Astragalus*, the other *Oxytropis*) sometimes found growing in the same environment, may be the result of later convergent evolution. The present single-character separation could be giving monophyletic groups. It seems a promising subject for phytochemical (and other) studies, but living material of the species pairs would be difficult to get.

It is evident that many infra-generic classifications are unsatisfactory because they are heavily weighted and therefore often unnatural. However, later monographers, tackling the same genera, have often started by accepting the traditional higher groupings and, by working downwards, have tried to improve matters within those groupings. Accepting 'received groups' is clearly not the best way to revise genera. They must be revised from the species upwards, recognising species-groups and trying to weld these together into higher natural subsections or subgenera (Hedge 1976).

FAMILIAL LEVEL. The family itself is a category of great practical importance, since we need to identify it before we can name an unfamiliar genus and thus reach a binomial. In the Angiosperms the family, like the subclass (Dicotyledons/Monocotyledons), genus and species, is one of the four most helpful signposts on the painful road to species identification. The status of many families (as well as their content and relationships) is in a state of flux, much of it brought about by phylogenetic speculation. The number of currently recognised families varies between 321 (Thorne 1976) and 439 (Takhtajan 1969), mostly due to splitting or lumping, only some of which involves different opinions on relationships. Even for the Ranunculaceae, Hutchinson, Cronquist (1968), Takhtajan and Thorne all adopt different parameters. Indeed it is often difficult to find out what genera different taxonomists' families contain. The best annotated recent systems in this respect are those of Hutchinson (1959) and Melchior's 8th Edition of Engler's *Syllabus der Pflanzenfamilien*, vol. 2 (1964).

Looking at the various Angiosperm systems published over the last 30 years, one gets the impression of great disagreement, especially with regard to relationships. Nevertheless, for the Angiosperms as a whole, the measure of agreement is much higher than one would expect from a casual inspection of recent systems. According to J. Cullen (unpublished), the 'noise' created by the diverse phylogenetic arrangements, the different circumscriptions, and the c. 30 families of uncertain relationships, obscure the considerable measure of agreement on the affinities of the majority of families as assessed on a 'pair-bond' basis. Eighty percent of the family pairs stay linked together in the same way in 5 or more of the 7 systems he analysed [from Hutchinson (1959) to Thorne (1976)].

Thorne's present system (1976) is the most aberrant, in both relationships and rank, of recent systems. He does, however, set out his general principles, and caps them by 7 'strong convictions or concepts' concerning his classificatory procedures. I find myself in disagreement with some of the latter. One of his convictions requires consistency of treatment in the size of the gaps separating families, irrespective of family size (cf. my remarks on p. 327). Another of Thorne's convictions does not allow tradition to influence classification. Some results of applying these opinions at family level are the recognition of a larger Liliaceae (divided into 24 subfamilies) than anyone has ever recognised before, the inclusion of Apocynaceae in Asclepiadaceae, and of Umbelliferae in Araliaceae. I do not deny that there are intermediate states between the linked families just mentioned, but they are too few to out-balance the practical advantages of maintaining them as separate families to which you would still need to turn in order to trace the literature on their genera. Fortunately, he does not always follow his avowed convictions. If he did, he would surely have included the Gesneriaceae in the Scrophulariaceae (as he does with the Orobanchaceae), instead of retaining the Gesneriaceae as a large separate family.

Above the family level: Orders and Disorders

Above the level of the family we are up to our necks in a quaking bog of orders, superorders, and (in the case of Thorne) suborders (often other taxonomists' orders). What is the purpose of this elaborate, still unstable, supra-familial superstructure? If it is intended as a guide to finding a family in the taxonomic system, it usually fails, particularly at the superorder level. The intention of its modern exponents, however, is evidently to construct an overall classification that expresses the Angiosperm's *phylogenetic* relationships. As Heywood (in Kubitzki 1977) expresses it: "There is an inbuilt conflict involved in constructing a scheme that attempts to express both the dynamical/historical phylogenetic component and a static horizontal present day classification, which makes most of the conventional phylogenetic tree-like diagrams conceptually suspect." Most such diagrams are, in fact, backward projections of present-day classifications. Take away the tree or shrub, and the broadly phenetic classification remains.

The present-day orders vary from being rarely very natural (e.g. Zingiberales) to amorphous and heterogeneous (Violales, sensu Stebbins, 1974), or monotypic in the case of very isolated (sometimes monogeneric) families (e.g. Rafflesiaceae). Heywood (in Kubitzki 1977) suggests that, so far as a retrieval system is concerned, it might be better to dispense with orders and have instead some informal higher groupings of families in the nature of polyphyletic grades (instead of speculative clades)—see note at the end of this section. Such grade groups were, in fact, used by Lindley, De Candolle, Bentham & Hooker, Engler & Prantl, Benson and others, and have helped us to find our way about the Angiosperm maze. I am doubtful, however, if the order (as the most commonly used category above the family and below the Dicot/Monocot division) should be abandoned. It is a long-established grouping that brings together, more often than not, related families. For that reason it seems useful to retain the order for studying family relationships and the position of genera of doubtful affinity; it is helpful for teaching purposes, and, in so far as the families within their order are patristically related, may prove economically useful.

If we keep up the order, however, it would seem sensible to recognise orders that genuinely have an internal coherence—not very large ones that contain families of very doubtful affinities. As done at present, very isolated families could be treated as monotypic orders, or perhaps even left *incertae sedis*, as Bentham & Hooker did for the Salicaceae, in the hope that further studies may establish definite relationships. Thorne's recognition of only 9 Angiosperm genera and 1 family (Goetzeaceae) as *incertae sedis* seems remarkably optimistic.

The superorder is a singularly unhelpful category. It is virtually useless for identification purposes (being differentiated mainly on unevenly sampled micro-characters or phytochemical features), and highly suspect as a patristic grouping. Cronquist, Takhtajan and Stebbins recognise 6 superorders in the Dicotyledons and 4 in the Monocotyledons; Thorne 16 in the Dicotyledons, 5 in the Monocotyledons—perhaps a more realistic approach. However, at present the superorder is a sack into which a variety of families have been stuffed by different taxonomists, often with scant regard for gross morphology and strongly weighted by phylogenetic speculation. I cannot believe, however, that the superorders bear much relationship to the evolutionary history of the Angiosperms, which was probably infinitely more complex than these few amorphous sacks suggest.

Judging by the Hamburg symposium on evolution and the classification of the higher categories (Kubitzki 1977), we are in for a long battle over supra-familial classification. In terms of practical application and economic value, is it worth the amount of time and effort being devoted to it, when good generic monographs and tropical Floras are needed so much more?

For the identification of families, it will probably always be easier to bypass the orders and superorders in favour of an artificial key to the families themselves, whether or not we start with the fairly natural Dicot/Monocot division. The most comprehensive dichotomous key to the families on a world basis is that of Hutchinson's (1967) with (I am told) a more than 75% success rate; however, its small unnumbered indentations make it easy to lose one's way. A punch-card key, like that of Hansen & Rahn (1969), may be expected to achieve a higher success rate, though scoring for subtle differences is difficult by this method. Formula ('multi-access') keys have proved successful in Davis's *Flora of Turkey* for identifying genera in the Umbelliferae and Compositae, but I doubt if they could be so effectively applied at ordinal, familial, or specific level—at least not in the form we used.

Note: Herbarium taxonomists find grade-groups useful in placing a plant in its family, particularly if the system is the one adopted in the herbarium in which they work. However, grade-groups are an unreliable guide, because the distinguishing characters used in a conspectus often only apply to part of the families described as possessing those features. One would have difficulty, for instance, in tracing *Kalanchoë* to the Crassulaceae, or a phyllodic *Acacia* to the Leguminosae in Bentham & Hooker's Polypetalae—ser. Calyciflorae—'cohort' (order) Rosales. However, in the majority of cases the Bentham & Hooker system is probably easier to use for running down a family than any other synopsis. When it fails (as it often must), we need to turn to a modern family key—or a well-informed colleague. The more phenetic our classification becomes (with the difficulties compounded by the influence of phylogenetic speculation on the content of orders and superorders), the more impossible it is to construct a synopsis that can be used both as a path-finder and as a ground plan of a natural system. We now seem to have passed the point of no return, with the almost total divorce of identification from classification, particularly above the family level.

THE SPECIES LEVEL AND BELOW

Taxonomists themselves, plant breeders, cytologists, anatomists and phyto-geographers are among those scientists who are most interested in having a phenetic (or 'natural') classification of organisms. A classification based on overall similarity will not only have the highest predictive value, but the best chance of being consistent with evolutionary relationships. However, there is no doubt at all that the service most required from taxonomists by the general public is the provision of the correct names for species; indeed, this basic service is also needed for the scientists I have just listed, as well as for ecologists. The correct identification of species is therefore the taxonomist's prime public responsibility, as those struggling to do research in under-staffed (or even over-staffed) herbaria know only too well.

Above the level of the species, at least to family level, the hierarchical position of taxa (even monotypic genera or families) mainly rests upon the degree of morphological difference. At the species level and below, however, there is an abrupt shift in the way the ranks are applied. In the recognition of species, subspecies and varieties other criteria are also taken into account. These include the degree of crossability, geographical distribution and ecological preferences.

It has been pointed out by Simpson (1961) that, *above* the species level, there is discontinuity both within and between taxa. In sexually reproducing organisms, there is continuity of variation and breeding pattern *within* species, whereas *between* species there is external discontinuity in these features. This is, in fact, an 'ideal' situation that is not always realised in nature, though the statement may stand as an acceptable generalisation. However, it probably applies better to animals than to plants, perhaps because the mobility of the former is counter-balanced by strong behavioural barriers to inter-specific mating; in the Angiosperms the frequent occurrence of polyploidy also tends to break down intersterility barriers. In this paper I am not going to discuss the almost insoluble problem of classifying apomicts.

In the higher plants every gradation occurs from full intersterility between taxonomic species to full (at least potential) interfertility, though in the latter case external barriers frequently operate in nature to maintain the relative integrity of the species. Nevertheless, more or less fertile hybrids commonly occur between some traditionally recognised species in Britain (e.g. in *Geum*, *Quercus*, *Salix*). In assessing the taxonomic treatment of such situations two considerations must be taken into account: the degree of morphological distinctness between the 'pure' species, and the extent to which hybridisation obscures their limits in nature. As typical *Geum urbanum* and *G. rivale*, and, to a lesser extent, typical *Quercus robur* and *Q. petraea*, differ in several characters, it seems justifiable to go on applying binomials to them. It is the usual practice to refer to such hybrid populations as hybrid swarms, unless they have become so stabilised as to be treated as species of hybrid origin, like *Quercus fusiformis* in N America. Breeding barriers within *Quercus* (a homoploid genus) and *Salix* are notoriously weak, and we would have very few species of oaks and willows left if we used crossability barriers as the best criterion for specific rank. In the case of *Silene dioica* and *S. alba*, which have different ecological preferences, the morphological differences are less striking. On the Continent, however, three subspecies of *S. alba* can be recognised (some of them extending far beyond the range of *S. dioica*), so there seems a good case, on grounds of convenience, for maintaining *S. dioica* and *S. alba* as species.

In the majority of cases (as in the inter-specific hybrids in *Geum* and *Silene* mentioned above) hybridisation occurs mainly in disturbed 'neutral' habitats, where neither parent is as well adapted as the hybrids, and competition weaker. In Turkey, considerable hybridisation seems to be taking place between what I am treating as subspecies of *Linaria genistifolia* and *L. kurdica* (Davis 1978), breaking down the differences that characterise them in their more natural and isolated localities. This situation is common in many species with 'weedy' tendencies. Indeed, selection for variable hybrid swarms may be on the increase. During the present century the effects of man and his flocks on the environment have accelerated to such an extent that there may be selection for *non*-stabilisation: the creation (if only temporarily) of 'anti-species'!

Both Flora writers and monographers need a practical species concept, because adequate experimental evidence (and even field observation) is frequently lacking; *force majeure*, taxonomists have to deal mostly with 'morphospecies'. Even when we have information on crossability it is mainly useful in tipping the balance in cases of uncertainty of treatment. Species should differ from their close relatives in at least two well-correlated characters—i.e. an acceptable degree of difference. (This is more than some genera may differ in—see *Oxytropis* and *Astragalus* on p. 331). Some would claim that one morphological difference, correlated with a chromosomal one (especially in ploidy level) justifies specific rank. Provided there is a difference in ploidy, Löve is apparently prepared to dispense with the morphological difference. However, we seldom (if ever) know how constantly exomorphic characters *are* correlated with cytological or genetic ones—in many cases an assumed correlation breaks down when more material is examined (e.g. *Monotropa hypopithys* $2n=48$ and *M. hypophegea* $2n=16$). In dealing with the flora of the Tropics, however, we seldom have any direct evidence of internal breeding barriers. For the majority of plants, binomials must be applied to representatives of populations that can be morphologically distinguished from one another, allowing perhaps for some degree of hybridisation, especially in disturbed habitats. In the case of completely allopatric species there may be slight morphological overlap due to homologous variation, or even resulting from clinal variation or introgression in an earlier period of sympatry.

Species, as they occur in nature, are the taxonomist's building bricks, to which binomials are applied for convenience, whether they are potentially inter-sterile or not. Geographical isolation (allopatry) has sometimes been wrongly used to support the recognition of a species. Although we expect subspecies to be largely allopatric, species can be allopatric or sympatric. On the other hand, if two closely related populations, with an acceptable degree of morphological difference, are sympatric and not separated by habitat preferences, we may assume that some barrier to interbreeding is operating and specific separation might well be justified. In the case of fully allopatric taxa, it is often a matter of opinion as to which rank is applied, though in borderline cases experimental evidence on the ability to exchange genes has been used to tip the balance (e.g. the recognition of *Nigella icarica* in the

N. arvensis complex, Strid 1970). Ehrendorfer (1971), however, is quite prepared to accept different chromosome races within E Mediterranean species of *Galium*, some of them at subspecific rank—a commendably practical approach.

Below the rank of species, *Flora Europaea* only recognises subspecies. This editorial policy, however, was dictated by lack of space in a large regional Flora. Personally I find it usually helpful to employ both subspecific and varietal rank in floristic work, but there is no generally acceptable distinction in usage. Most of us these days would probably be prepared to recognise morphologically distinguishable regional races as *subspecies*, with or without some degree of morphological or geographical overlap. When the area of subspecies is large, an acceptable difference can be small. *Parentucellia latifolia* (Scrophulariaceae) has purplish (rarely yellowish) flowers in Europe (subsp. *latifolia*) and yellow flowers in SW & C Asia (subsp. *flaviflora*); no other constant difference can be detected, and both are apparently sympatric on Cyprus (Hedge in *Notes R.B.G. Edinb.* 36:10–11, 1978). Hedge (*l.c.* 23:550–561, 1961) recognised three allopatric subspecies of the endemic Anatolian *Saponaria prostrata*. One of these conspicuously differs from the other two annual/biennial subspecies (between whose areas it grows) in being perennial, with persistent sterile rosettes, but otherwise differs from the other subspecies only in having slightly larger flowers. It would be particularly interesting to know the cytological situation in the three subspecies, since a difference in ploidy level of the perennial would (in my view) support specific separation.

Article 26 of the *International Code of Botanical Nomenclature* can result in a rather unfortunate situation. If you describe the first infra-specific taxon within a species, you create (whether you want to or not) an autonym for the rest of the species. This means that if a peripheral variant is treated as a subspecies or variety, the rest of the species (containing its type) is automatically given the same rank (as an autonym without authority), however variable and unequivalent it may be in relation to your new subspecies or variety. Thus the biological pattern is obscured by a pseudo-standardisation enforced by the Code.

Apart from regional subspecies, we frequently find smaller, but recognisably different *local* races too. These may sometimes occur within the broad geographical range of a subspecies. A good example is the East Mediterranean *Geranium cinereum* subsp. *subcaulescens* (with long white hairs present on the calyx, instead of entirely adpressed-pubescent in the western subsp. *cinereum*). Subsp. *subcaulescens* is itself differentiated into local *varieties*, differing mainly in leaf shape, habit and flower colour (Davis, *Fl. Turkey* 2:471, 1967). In practice, however, varietal rank has probably been more often used for small races that grow *outside* the range of the regional subspecies. I suggest it might be better to treat both regional and distinctive local (small-area) races as subspecies (as in *Teline monspessulanus* in the Canaries, Gibbs & Dingwall 1971), except for the less common situation I have described for *Geranium cinereum*. It should be pointed out that regional subspecies are not necessarily better distinguished, morphologically, than local varieties. It is more a matter of distribution pattern as to which rank is used.

Varietal rank can also be conveniently applied in those cases where a variant forms local populations scattered throughout the range of a species or subspecies. *Poa alpina* var. *vivipara* provides a good example; however, in this case the populations, though morphologically similar, are not always cytologically equivalent.

It will certainly lead to a loss of information on species variability if local variants are not recognised at all. It is just at this stage in evolution—the ecotype that has become morphologically differentiated as an isolated local population—that further homoploid differentiation is likely to occur. It is difficult to visualise how a widespread coherent subspecies could evolve into a separate species unless part of it gets cut off as a small isolated population. Much of the mosaic pattern of endemism in Anatolia (a country with diverse topography and climates) may well have originated in this way.

Unfortunately varietal rank has also been used in other senses than for the local populations I have already described. It has been used for striking variants (usually discovered in herbaria) to which taxonomists want to draw attention. Some of these, when better understood, may turn out to be extreme modifications (e.g. the effect of shading or grazing) that should not have been formally named at all, or they may even turn out to be species. Other varieties, e.g. *Pimpinella saxifraga* var. *dissecta*, *Lathyrus vernus* var. *tenuifolia*, are striking sporadic variants that are part of a polymorphic population, and would be better treated (if at all) as forms. Ascherson & Graebner's *Synopsis Mitteleur. Fl.* (1896–1938) set a pattern of over-elaborate infra-specific classification that penetrated the first edition of Hegi's *Illustrierte Flora von Mitteleuropa* (1906–31) and presumably encouraged the eccentric pulverisation developed in Rouy & Foucaud's *Flore de France* (1893–1913). The supreme example of nonsense taxonomy is perhaps Fedde's account of *Papaver rhoeas* (*Pflanzenreich* iv 104:295, 1909), in which varieties and subvarieties are described under leaf shape, flower colour, indumentum, etc., so that the same specimen can be assigned to several different taxa!

Flora writers are naturally reluctant to change the rank of infra-specific taxa without good cause. That job is better left to monographers. When varieties are described, however, it would be very helpful if the taxonomist would indicate the way in which he thinks the rank is being used. Fernald (ed. 8 of Gray's *Manual of Botany*) only used variety and form, the first often being equivalent to subspecies.

Forms (*formae*) in the sense of sporadic, often single-gene variants, are to my mind best not given formal recognition. The population concept of modern systematics implies that we should apply formal names only to populations, not (knowingly) to individual variants that are part of a polymorphic population's fluctuating variability. By doing so botanists may end up by naming single genes, which seems to be the case with the forms of *Viola riviniana* recently treated by Valentine (1975). He describes the same form (based on the production of adventitious shoots from the roots, associated with the possession of supernumerary chromosomes), using a different epithet for it under each of two varieties. If it is thought necessary to tag genes, surely it is better to do so informally, e.g. *forma radicibus soboliferis*, or by a short descriptive phrase in English, German or French.

However, the form, in the sense of a simple genetic variant, has important evolutionary potential. If an albino or a glabrous-fruited variant, for instance, occurs as a double recessive, it may, by dispersal outside the parent population, build up a population homozygous for that particular gene. If this population is constantly (say) white-flowered or glabrous-fruited, it would be eligible for varietal rank. Further differentiation *in situ*, or as a new satellite population, might eventually lead to a biological situation that would justify recognition as a subspecies, or (in association with other accumulating differences) a species. Although we do not know the cytological facts, this may well have happened in a S Anatolian *Omphalodes* (Boraginaceae). *Omphalodes ripleyana* is a white-flowered, cavernicolous plant with toothed-winged nutlets, apparently derived from the disjunct *O. luciliae* which extends from Greece to SW Iran—a blue-flowered species of open limestone rocks, and one in which rare albinos occur.

Below the species level, infra-specific names are often very difficult to trace, creating nomenclatural problems that take up much valuable time that would be better spent on the plants themselves. Burtt (1970), discussing the "muck-heap of two centuries of unindexed and inadequately described epithets", suggests that the Code will in time come to "accept it as disposable refuse". If that day comes, perhaps we can all start again, in a more realistic and sensible manner.

Taxonomy deals with natural diversity. This does not mean that we need to classify *all* that variation formally, either below the species level or above it. If a small genus contains only three species, each very distinct but evidently congeneric, there is no need to create a section for each of them—a note emphasising their distinctness will do the job just as well, without adding further to the sediments of nomenclature.

Taxonomists usually classify organisms because they enjoy doing so, but they should not be too self-indulgent about it. Classifications are for other people. As Burtt (1964) points out, because we are actually classifying organisms related by evolution, what we need is a classification for the *study* of evolution (not one based on assumed phylogenies); this is also the one that serves most of those "general purposes" we read about. At present a broadly phenetic, "omnispective system" (by which Blackwelder, 1967, means the "all-considering system" in current use by most taxonomists) best fits the bill. It is a Phoenix with a difference: continually rising from the ashes of its predecessor and, if taxonomists stoke the fire properly, burning with a more luminous flame. Basically the same, yet always different.

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