A TAXONOMIC CRITIQUE OF RECENT NUMERICAL STUDIES IN ERICALES AND SALVIA

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ABSTRACT. A general assessment is given of the taxonomist's difficulties in accepting a novel classification, especially one reached by using numerical techniques based on a measurement of overall similarity. The inclusion of untried characters: the total exclusion of others on which the classification of the group has previously depended: the use o characters, valid enough within a narrow affinity, through a larger taxonomic group where they have almost certainly arisen more than once: all these aspects are open to criticism. It is shown in particular that the application of these methods to *Salvia* has resulted in the association of species of no near affinity and the sundering of others closely allied. In Ericaceae one of the main weaknesses that invalidates the proposed classification is the sampling of the taxonomic units. Genera critical to an interpretation of the results were omitted and the representation of others was inadequate. Choice of character states which do not properly reflect the biological situation is also a possible source of distortion.

GENERAL REMARKS

There have been two notable tendencies in taxonomy in the last twenty years. One is concerned with the expansion of the range of characters utilized, the other with the use of sophisticated numerical techniques. This latter aspect of the subject is in a state of rapid ecological succession, almost each paper is a seral stage contributing to its own replacement by an improved method. However the taxonomic results themselves are, when published, less transient and exert something of a tyranny over other workers. What is published all too easily achieves authority. Sooner or later the taxonomist finds that groups in which he has a special interest have been used in experimental work of this kind, and then comment becomes unavoidable.

We at Edinburgh are particularly affected by two sets of studies: one on *Ericales* (Watson et al., 1966, 1967), the other on *Salvia* (El-Gazzar et al., 1968). Tyranny has been exerted partly through the medium of Sneath, who says with apparent approval at an international symposium (Sneath 1969, p. 14) that these authors "have examined the performance of numerical taxonomy with angiosperms, and they conclude that even the less satisfactory numerical techniques can provide classifications that are better than many of the traditional taxonomies". We disagree.

The present paper is in effect three chapters written more or less independently: these general remarks (B. L. B.), comments on Ericales (P. F. S.)* and comments on *Salvia* (I. C. H.). However, the whole has a substantial measure of tripartite assent.

Two different approaches to the choice of taxonomic characters for use in a numerical assessment are possible. At one extreme is the pure taximetrician who wishes to start his study without any taxonomic basis, or bias, other than that necessary to define his chosen group. He must treat all characters as equal because no evaluation is possible until the beginnings of

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* Work extracted from studies on Ericales carried out while in receipt of a Ph.D. studentship from S.R.C.

a classification have been made. His selection of characters should, therefore, be taxonomically objective, influenced only by their accessibility and their suitability for scoring in an acceptable form.

At the other extreme the most conservative orthodox taxonomist will not wish the final classification to be in any way influenced by a character that he does not accept as taxonomically reliable. These extreme types may be mythical, but the cleavage into two main schools of thought does exist.

The orthodox taxonomist's viewpoint is easily explained. He is unfamiliar with the new techniques and they have not yet inspired confidence enough for a quite novel classification to be acceptable unless it is simply and demonstrably better than the old. He will have already formed an opinion about the value of certain characters and the inclusion of those that he does not accept as indicative of affinity, on the scale of the study being made, will prejudice him against the result.

For example, in the family Gesneriaceae, within the affinity of *Boea* and allied genera the presence of a bilabiate calyx (compared with one divided equally into five segments) is a feature of taxonomic value and helps to delimit the genus *Dichiloboea*; if, however, the whole subfamily *Cyrtandroideae* is the subject of study, it will be found that this character is also present in a few species of *Didymocarpus*, *Chirita*, *Trisepalum*, *Petrocosmea*, *Cyrtandra* and probably elsewhere. These plants are in no way closely related on other criteria and to attach any value to this character in an overall study of the subfamily seems ridiculous. Its inclusion in a numerical assessment would need to be accompanied by the assurance that the computer programme will reject the sporadic occurrence of such a character as evidence of affinity. This cannot always be given.

It is clear that the choice of characters must be directly linked to the scope of the project; it may be very desirable to change characters at different levels of study. In the above example the taxonomist would as justifiably demand the inclusion of the calyx character in classifying *Boea* and its allies as he would reject it in the classification of the subfamily as a whole.

This leads immediately to the question whether it is useful to produce new classifications that deliberately exclude characters previously ranked as important. It is particularly relevant to the assessment of the recent work on *Salvia* (see below). Several studies have, indeed, shown that the use of different suites of characters may result in different groupings (see Crovello, 1969 and further references there).

Characters of micromorphology (such as type and distribution of idioblasts, stomata, cell inclusions etc.) have become popular because they can often be easily obtained off herbarium material. Such new characters have indeed proved of distinct taxonomic value in several non-numerical studies (cf. Dormer, 1962; Watson, 1965; cf. also Bokhari on sclereids in *Limonium*, see p. 43 and Bokhari & Burtt on *Cyrtandra* see p. 11; numerous other examples could be quoted). They have the advantage that they are easier to handle than the continuous and complex variables involved in corolla shape, while leaf shape may be highly variable on one plant. Nevertheless these are additional characters not lightly to be used *instead* of flower, leaf and fruit; some of them prove of trivial taxonomic importance except within very narrow circles of affinity and they need to be evaluated in each group independently.

The theoretical basis for the isocratic use of characters has never been that all *are* of equal value: it is that the subjective element in deciding which are more important is so great that it is preferable to *treat* them all as equal (cf. Burtt, 1964, p. 15). It is rather ironic that this viewpoint should gain in favour during a period in which much more factual knowledge is becoming available about the relative value (information content) of characters. For instance the importance of the macromolecules of the proteins in comparison with that of the smaller molecules often used in chemotaxonomic studies has recently been stressed (Sibley, 1969, p. 322). Another example: in *Streptocarpus* flower patterning is of taxonomic importance and has been shown (Lawrence, 1958) to be controlled by a complex supergene; flower colour, under the control of a number of separate genes inherited independently, is relatively unreliable.

The objectivity which was to be the great contribution of numerical methods, is in fact of minor importance. Blind (objective?) selection of characters just will not work. Once the characters have been selected by the taxonomist all the indications are that he does not do too badly on his own, for numerical assessments from the earliest (Michener & Sokal, 1957) to some of the latest (Prance et al, 1969) have suggested little change.

Sneath concludes a recent paper (1969, p. 18) by saying "it should be noted that some way is now needed *to integrate* voluminous new data now being accumulated from all sources *into the body of taxonomy*. Numerical methods offer the only satisfactory way of doing this". The *italics* are mine. These words seem to envisage the incorporation of all new data as active components into the formation of classifications. It is by no means certain that the inclusion of more and more characters in a classification will effect improvements.

We are seeking not merely to classify plants but to learn about them. The classification is both an end product and a tool. We need stable classifications against which the distribution of other characters (not used in their construction) can be studied. It is just from the tension between a classification and characters discordant with it that we learn about plants. It is an old tenet of taxonomy that geographical distribution must not be used as a character, for the groups so formed would be invalid in phytogeographical studies. Parallelism between groups is one of the best sources of evidence for the existence of selective pressures and evolutionary trends. The classificatory tool must not be blunted by including characters of independent origin as similarities.

This was written before reading Crovello's recent paper (Crovello, 1969) but it seems to me that his suggestion of the comparison of different phenograms as a source of biosytematic hypotheses is in many ways a sophisticated version of the idea expressed above, that we learn not merely from the classification, but from the tension between it and discordant data.

Sneath is, of course, perfectly right if he means that the computer will have to come into use eventually for information storage so that all the new data can be attached to the relevant taxa and retrieved at will. But that is a very different matter from the integration of this data into the taxonomy.

Any "conclusions" at this stage would be ridiculous, but one or two points demand emphasis. Sampling, if it must be done at all beyond the level dictated by inadequate material, must be selective, so that all problem species or genera are included. Checks on identity are just as important in this work as any other: the inclusion of the same species under different names, or the "representation" of a genus by species which are no longer placed in it (both occur in the papers under discussion), can only destroy confidence in the results. It is, indeed, to be hoped that the full data, with references to the specimens used, are always permanently preserved so that they can be consulted by later workers if need be.

Numerical methods will certainly become of great importance in taxonomy, but they are likely to be of most value in the intermediate phases of the work. A lot of hard taxonomy on orthodox lines will have to precede any numerical assessment and a final taxonomic evaluation will probably remain essential. The advent of the computer does, however, make feasible an attack on large compact groups of world wide distribution (one thinks immediately of the ragworts—certain sections of *Senecio*), which have just never been tackled as a whole. As to the further use of similar methods to develop various sorts of evolutionary hypotheses: this comes after the classification has been made, although, of course, to say this is not to imply that the classification itself will ever be final.

THE ERICALES

INTRODUCTION

Watson et al. (1967) proposed a revised classification of the Ericaceae (from the tribal level and above) as a result of their studies on fewer than 96 species from about 43 genera of the family; this was part of a larger study on the classification of the Ericales. This number is only approximate, since some of the specific and generic names listed are synonyms of those occurring elsewhere on the list given. Information on 37 characters was collected. These characters were qualitative, ordered or disordered multi-state and quantitative. The programme used computed an overall non-metric similarity coefficient between all pairs of the O.T.Us being considered, and then a dendrogram was constructed using an agglomerative centroid sorting strategy. The level at which two groups joined was calculated from the average similarity between all the O.T.Us of the two groups involved.

The present comments on the proposed classification and the process by which Watson et al. arrived at this classification arise out of work carried out in an attempt to elucidate some of the relationships within the family (Stevens, 1969); it has involved detailed study of over 550 species of the family, in a number of cases from several collections. It is not proposed to present a revised classification here; this will be done elsewhere.

DISCUSSION

1. *Sampling*. In any taxonomic study, suitable sampling is essential if reliable inferences and conclusions are to be drawn, and poor sampling has relatively more serious effects in taxonomic than in many non-taxonomic systems, since omitted taxa may completely change a classification. One is not dealing with a system whose members have to fall into predictable, discrete groups. Thus with 50% random sampling one is likely to solve well under 50% of the problems. No programme can get over this, although with careful selection of taxa one can ensure a better cover of the variability and hence get

out more robust groups, i.e. groups which change relatively little when further taxa are studied. Prance et al. (1969) sampled about 50% of the species of the Chrysobalanaceae in which they were interested; Watson et al. (1967) about 25% of the species and almost all the genera of the Epacridaceae and c. 2% of the species and about 40% of the genera of the Ericaceae. Poor sampling effectively reduces one's work to the level of that of the 19th century taxonomists who were working with much scantier material.

Many of the problems in the Ericaceae are posed by less well-known taxa. *Pieris swinhoei* and *P. phillyriifolia* both have seeds with unelongated testa cells, basal placentae, and geniculate or near geniculate filaments, whilst the rest of the genus have much elongated testa cells, apical placentae and their filaments are straight. Recognition of this sort of variation (paralleled by *Enkianthus subsessilis* when compared to the rest of the genus *Enkianthus*) helps one better to appreciate the variation pattern of the Andromedeae sensu Drude as a whole. None of these species is commonly cultivated. Watson et al. (1967) studied only 5 temperate species of the genus *Vaccinium* (including *V. oxycoccus*), a genus that is predominantly tropical and subtropical and has over 300 species. Only 5 species, out of perhaps 1,000, of *Rhododendron* were examined, and only c. 7 species of Ericaceae from the whole of S America were seen; there are hundreds of species of the Ericaceae on this continent, and it is full of problems for the student of the family (e.g. *Tepuia*, *Lateropora*, *Notopora*, *Gaultheria*).

Harrimanella (sometimes included in *Cassiope*) was not studied by Watson et al. (1967), yet its omission invalidates the important conclusions reached as to the relationship between *Calluna* and *Cassiope*, and hence between *Cassiope* and the Ericoideae. *Harrimanella* and *Cassiope* are very similar in flower and fruit, differing only in minor details of anther, corolla lobing and floral stomatal distribution (Stevens, 1969); they possibly have a similar *Allium*-type embryo sac development in common (Palser, 1952), and this is not found elsewhere in the family. *Calluna* differs greatly in all these respects —it has a basically different perianth arrangement, stamen, capsule and seed type. In anatomy and inflorescence there is quite a different picture; all three have different inflorescences, although that of *Harrimanella* is perhaps rather more distinct, being terminal, while the two others have axillary flowers. *Harrimanella* has homogeneous pith and acicular petiolate leaves, *Calluna* and *Cassiope* have *Calluna*-type pith and channelled, sessile leaves, or "acicular" leaves derived from the channelled type (Stevens, 1969). *Harrimanella* and *Calluna* agree in floral stomatal distribution and in having bast fibres associated with the midrib bundle of the leaf, but in epidermal type *Harrimanella* agrees with *Cassiope*. Many of the characters possessed by *Harrimanella* and not by *Calluna* and *Cassiope* are more common elsewhere in the Ericaceae.

Another interesting genus of ericoid facies, *Bryanthus*, appears by name, but was in fact not studied: the two species of *Bryanthus* listed (Watson et al., 1967) are referable to *Phyllodoce*.

2. *Number of characters*. Watson et al. (1967) attempt to classify the Ericales, recognising taxa from the family to the tribe, in one operation using only 37 characters. By the time the Ericaceae as a group have been recognised, three of these characters do not apply (all Ericaceae have 4

anther thecae, non-sheathing leaf bases, and they can hardly be said to lack a distinct leaf midrib, although this is perhaps debatable). The use of so few characters is questionable, although Watson et al. (1967) think that fewer characters than the 40–60 or more that are often suggested can produce a successful classification. This does not seem to have been the case in the Ericaceae (see below), although the small number of characters is only one of several factors which contribute to the failure of the classification.

3. *Choice of characters*. The choice of characters is a central problem in any taxonomic study, even non-numerical ones. Characters (such as seed wings, mentioned below) may not be strictly homologous in different plants, or the same character state (for example, the fleshy fruit) may demonstrably have arisen independently in different parts of the group under study. Methods of numerical analysis which are based on overall similarity are unable to discriminate between such characters and those which have arisen only once during the evolution of the group, although programmes based on analyses of character variance may be able to do so. Such problems are accentuated in studies, such as those on the Ericales, which involve diverse and isolated groups between which it is often very difficult to establish homology (see especially the difficulties encountered by Kendrick & Weresub, 1966, in their studies of the Basidiomycetes).

A few examples of this sort of problem within the Ericaceae may be given; they concern only those characters used by Watson et al. (1967). A superficially similar character which has a different structure in different parts of the family, (strictly non-homologous), is the "winged seed", which may be caused by a locally multi-layered testa (*Chamaedaphne*), by expanded cells at the seed margin (*Leucothoë*), by plates of cells (*Rhododendron canadense*), by the seed as a whole being compressed (*Elliottia*) or by the seeds being elongated (*Rhododendron—Hymenanthes* group). Even the three genera with expanded cells at the margin of the seed (*Rhododendron*, *Leucothoë* and *Enkianthus*) have few other characters in common, and have probably evolved this particular character independently. Although *Calluna* and *Cassiope* appear to have in common a very unusual leaf type, the similarity may be more apparent than real. The leaves of *Calluna* are tailed, those of *Cassiope* have auricles, and the epidermes are different in the two genera, so the *Calluna*-type leaf may not be homologous wherever it occurs.

Homologous characters, apparently involving the same tissues (which may, however, be produced by different morphogenetic pathways) but which are of independent origin, are the berry of *Pernettya* and *Arbutus*, and the drupe of *Arctostaphylos* and related genera and that of *Gaylussacia*; the members of the pairs, especially in the latter case, have little else in common. The adaxial leaf stomata to be found in *Calluna*, *Cassiope*, *Harrimanella*, some species of *Arctostaphylos*, *Rhododendron*, *Vaccinium*, *Bejaria*, *Epigaea*, and *Rhodothamnus* may be comparable as phenomena, but since the species involved have paracytic, anomocytic or tetracytic stomata and differ widely in almost all other details they are unlikely to be indicative of relationship. Any method of computation is going to produce a confused picture if too many such characters are used.

A taxonomist treats each taxonomic level independently; for each level he evaluates the characters anew, rejects some which are constant throughout the group and brings in new characters which can be used with confidence only in limited circles of affinity, since only there is their common origin certain. Hence a very large number of characters are used. Something along these lines, although without the addition of new data, was carried out in a numerical study by Throckmorton (1968). She reclassified the groups forming at the successively lower levels in the analysis independently and only after removing more or less invariable "outside" or "operational" primitives at each stage. A programme allowing one to reclassify at each level, adding new data, seems in some ways an ideal one to use since it would help to circumvent the problems of homology and parallel and convergent evolution.

4. *Delimitation of character states and errors in observation*. For the computer to evaluate similarities between taxa the character states for each character must be carefully defined. Watson et al. (1967) consider capsule dehiscence to be a two-state character "septicidal/loculicidal or both". If capsules dehisce both ways at once, it is not logical to include the intermediate type with either of the other two. Such a delimitation of states will obviously lead to an increased measurement of overall similarity between taxa with loculicidal dehiscence and those with the "intermediate" type; this may have been a factor contributing to the inclusion of *Kalmia*, *Phyllodoce*, *Epigaea* and *Rhodothamnus* in a group of the dendrogram which includes the Andromedeae sensu Drude. Although all members of the Andromedeae have loculicidally dehiscent capsules, those of the above genera, as well as others of the Rhododendroideae which do have loculicidal slits, are much closer to the septicidal type (Fig. 1). *Loiseleuria* is perhaps the nearest approach to an intermediate type, but even in this genus most sheets examined had capsules which were dehiscing predominantly down the septal radii (the capsule drawn shows the most extreme loculicidal dehiscence seen in any member of Rhododendroideae). Thus the "intermediate" type of capsule should be scored with the septicidal type.

From Hara's work (1956 & 1958) it seems that there are two main leaf types in the Ericaceae from the point of view of development: convolute and revolute. The Ericoid leaf, as well as that of *Calluna*, falls into the latter category. Hence scoring leaf type as "Ericoid (rolled, needle)/Calluna-type (broad)" is misleading. This emphasises the fact that, both in ascertaining homology and in the scoring of characters, the ontogeny of a character, insofar as it is known, may usefully be taken into account.

In the character of stamen position, "epipetalous/free/adnate to the corolla" it is not clear how the first and last states differ, although the last may refer to those genera whose stamens are weakly attached to the corolla for a fraction of a millimetre.

Finally, it might have been better to consider nodal anatomy as a three-state character (unilacunar/trilacunar/multilacunar), rather than as a bi-state character (unilacunar/tri- or multilacunar).

There are about 10% discrepancies when Watson's (1965) data on stomatal distribution and type in leaf and flower are compared to those obtained here (Stevens, 1969), and although some of these may be due to infraspecific variation in these characters (as has been found in foliar stomatal distribution in *Vaccinium myrtillus* and *V. amblyandrum* and floral stomatal distribution in *Chamaedaphne calyculata*, *Gaultheria suborbicularis*, etc.) it does seem that

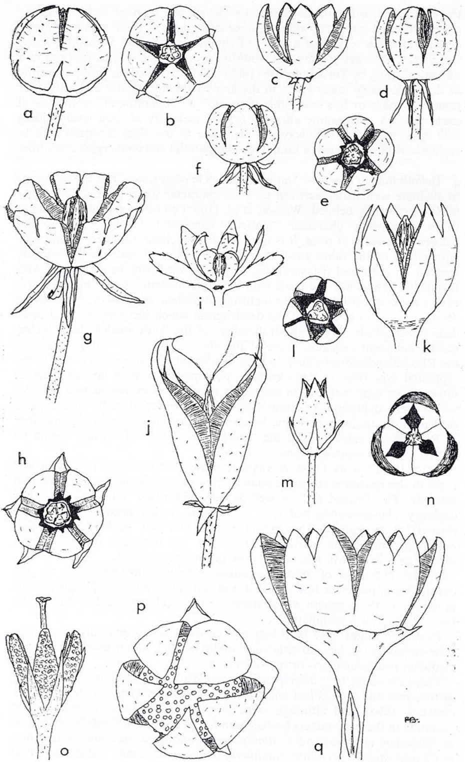

FIG. 1. Some capsule types of the Rhododendroideae: a, *Kalmia latifolia*, x 5; b, the same, from above; c, *K. hirsuta*, x 6; d, *Rhodothamnus chamaecistus*, x 3; e, the same, from above; f, *Kalmiopsis leachiana*, x 6; g, *Phyllodoce aleutica*, x 6—old capsule; h, *P. nipponica*, x 6—from above; i, *Diplarche multiflora*, x 6—septifragal; j, *Daboecia azorica*, x 5; k, *Loiseleuria procumbens*, x 7·5; l, the same, from above, x 5; m, *Leiophyllum buxifolium*, x 6; n, *Tripetaleia bracteata*, x 3—from above; o, *Ledothamnus guyanensis*, x 6; p, *Epigaea asiatica*, x 3—from above; q, *Bejaria racemosa*, x 5.

some of them are due to his misobservations. The most important ones are the type of stomata on the leaves of *Gaultheria*, *Pernettya* and *Elliottia paniculata* (the last named and *E. racemosa* have paracytic stomata, the only members of the Rhododendroideae at present known to have them), calyx stomatal distribution of *Pieris* sensu stricto, and the corolla stomatal distribution of *Vaccinium oxycoccus*, *Zenobia*, *Agauria*, *Arbutus*, *Arctostaphylos*, *Elliottia*, *Cladothamnus* and *Ledothamnus*. Discrepancies as to the type of stomata on the leaves of *Gaultheria*, *Pernettya*, *Chiogenes* and *Chamaedaphne* may be partly due to differences in definition, since in many species of these genera the stomata are not paracytic in the sense that the accessory cells are obviously different in size and/or shape from the surrounding epidermal cells. Indeed, many species in these genera have only 60% or fewer configrations which could be called paracytic, even if only the position of the cells is considered.

Watson (1962, 1965) & Watson et al. (1967) mention only two types of stomatal orientation in the Ericales, longitudinal and irregular. There are three: in *Bejaria*, *Rhododendron* section *Choniastrum*, all the *Ericoideae* seen, *Ledothamnus* etc. of the Ericaceae and *Lysinema conspicuum* of the Epacridaceae (see also Simon, 1891; other members of the genus have not been examined) the long axes of the stomata are at right angles to the long axis of the leaf.

The combined effect of these misobservations and the unsatisfactory scoring of some of the characters cannot be negligible. Fisher & Rohlf (1969) found that the fine structure of the dendrogram was considerably affected if they scrambled as few as 10 out of 74 characters obtained from *Drosophila* pupae, i.e. they assigned the records of the character states to the O.T.U.s at random and so simulated errors of homology and observation. They thought that the maximum tolerable number of such non-homologous characters was 6 out of 74.

5. *Dendrogram and classification.* It is generally recognised that the taxonomist must have the final say in just what parts of the dendrogram, or whatever structure the computer produces, are to be recognised in the classification proposed. Watson et al. (1967) recognise that there are likely to be "migration problems" in the programme which they were using, i.e. an O.T.U. irrevocably joins a group because of a high similarity value between it and one member of that group, although the average similarity value is higher between this O.T.U. and some other group. Nonetheless, there does seem to have been a surprising amount of rearrangement when the dendrogram and the classification proposed are compared (Fig. 2). One of the claims of numerical taxonomy is objectivity, and although the members of the Phyllodoceae are said to be "demonstrably" more similar to one another than to the other tribes, no further details are given. In the classification finally adopted, one cannot see any close relationship between fusion level on the dendrogram and tribal and subfamilial groupings adopted. The impression gained is that the classification proposed, in the Ericaceae at least, owes little to numerical methods but more to the evolving ideas on the classification of the Ericaceae expressed by Watson (1965, 1966) before a computer was used.

It is interesting to see that in the Epacridaceae the classification produced seems to be more sound, and it also shows good agreement with the dendrogram (Watson et al., 1966, 1967). This is probably due to the relatively much better sampling within this family, and also to the fact that the Epacridaceae are a much more homogeneous family than the Ericaceae, so problems of homology and convergent evolution are much more easily recognised and circumvented. Also the number of characters needed for a successful classification may perhaps be smaller.

It is not proposed to give here a detailed criticism of the classification of the Ericaceae finally adopted by Watson et al. (1967), but the following points may be noted. From what has already been said, it will be apparent that *Calluna* and *Cassiope/Harrimanella* make uneasy tribal bed-fellows. The inclusion of *Elliottia* and *Cladothamnus* with *Menziesia*, *Tsusiophyllum*, *Rhododendron* and *Ledum* in Subfamily II Tribe 1 is insupportable. The first

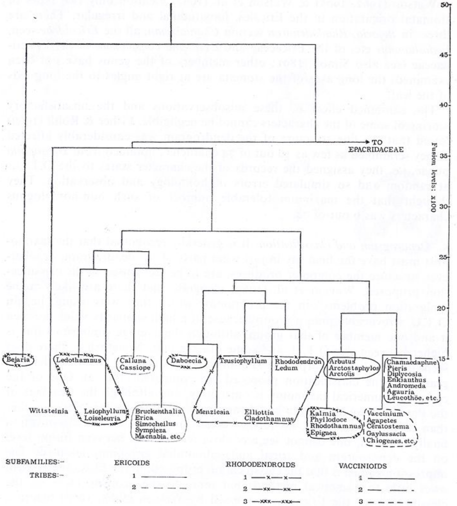

FIG. 2. The classification of the Ericaceae, after Watson et al. (taken from Fig. 1 & Table 5, Watson et al., 1967).

two genera differ from the others in seed type (cells of testa not elongated v. cells usually elongated), embryology (no chalazal endosperm haustorium v. this haustorium present), anther dehiscence (resorbtion tissue present, anther dehiscing by elongated slits v. no resorbtion tissue, dehiscence by at most short slits), bud perulae (none v. present) and pollination mechanisms. The insects pollinating *Cladothamnus* and *Elliottia* receive pollen on the dorsal part of the body (head to abdomen), whilst the bees visiting the other genera receive pollen on their undersides (possibly on their heads in *Menziesia* and *Ledum*). This is the result of the petals, stamens and stigma/style complex being arranged in quite different ways in the two groups. Finally, *Chiogenes* was included in the same tribe as *Vaccinium*. It smells of methyl salicylate, as do several species of *Gaultheria* but none of any of the genera included in the Vaccinieae. Its stomata are not really paracytic (see above); all the Vaccinieae seem to have truly paracytic stomata. The anthers of *Chiogenes* have two pairs of terminal awns whilst the appendages of the stamens in the Vaccinieae, where present, are paired or single, dorsal spurs. The ovary of *Chiogenes* is only half inferior, more superior than any species included in the Vaccinieae, although Palser (1961) notes that the vascular supply to the organs of the flower is even more congested than that in some species of *Vaccinium*. *Chiogenes* is usually included in *Gaultheria* (Airy Shaw, 1940; Sleumer, 1941), and this seems to be the correct position. A less-known species, *G. suborbicularis*, to a considerable extent bridges the gap between *G. hispidula* and *Gaultheria* series *Trichophyllae*.

Two of the suggestions made by Watson et al. (1967) are well founded. One is the reduction in the rank of the group of vaccinioid genera with inferior ovaries from subfamily or family, which all recent authors have adopted, to tribe; the other is the inclusion of *Epigaea* in the Rhododendroideae.

SAGES IN DISARRAY

GENERAL DISCUSSION

In the course of several years' work on the taxonomy of *Salvia* in south-west Asia, and during preparations for a revision of all the Old World species, I have found the basic sub-generic divisions recognised by Boissier (1879), Briquet (1896) and Pobedimova (1954) reasonably satisfactory and practical to use. The recent attempt by El-Gazzar, Watson, Williams & Lance (1968) to provide a sub-generic classification by computer techniques therefore merits some discussion because their results differ so fundamentally from any previous classification.

In a fairly cosmopolitan sample of about one hundred species, which represents somewhat more than 10% of the total number of species in the genus, they selected characters from leaf, calyx, stamen, bract, style and indumentum: 4 from the leaf, 6 from the calyx, 2 from the stamens, 2 from the bracts and 1 from the style. In all, 41 states of these characters were used. These comparative observations were then subjected to two basically different programmes, "Multiclas" and "Centlas". The results in both cases were essentially the same. Two main divisions were recognised: the first included all the species of the New World subgenus *Calosphace* and the second species from all other sections throughout the world. Within these two divisions, seven groups in all were recognised which completely cut across the 13 currently accepted taxonomic groups. Group 1 contained 17 species from 6 sections; group 2, 14 species from 4 sections; group 3, 11 species from 1 section; group 4, 13 species from 7 sections; group 5, 10 species from 3 sections. Groups 6 and 7 contained only species from subgenus *Calosphace*. Because these seven groups represent the main taxonomic conclusions and as the authors considered that they were a satisfactory arrangement, they are worth studying in some detail.

For this review of their results, two aspects of their groups were considered. Firstly, one pair of apparently dissimilar species was selected from four of the groups to determine whether they had more in common with each other than previously recognised. Secondly, two species, previously considered as close allies but in the numerical studies placed in separate groups, were examined.

1. *Dissimilar species*. The following species were selected: from group 1, *S. verticillata* and *S. aurea;* group 2, '*S. sylvestris*'* and *S. viridis;* group 4, *S. plebeia* and *S. bulleyana;* group 5, *S. dominica* and *S. aegyptiaca*. These species-pairs are all extremely unlike in facies and floral characters and it is remarkable that any methods of classification should link them in the same group. They were therefore re-examined using the characters of the numerical study. Several gatherings of each species were used. The table below, summarises some of these results, covering 5 of the 6 multistate characters used. Not included in the table are the qualitative characters of leaf, calyx, bracts, stamens and style which scarcely varied in any of the selected species-pairs; they are discussed below.

	Calyx type	Calyx veins: number	Stamen type	Calyx indumentum type	Leaf indumentum type
S. verticillata	4	13	1	1	1
S. aurea	5	12–14	4	1	1
S. sylvestris	4	13–15	4	1, 2	1
S. viridis	3/4	12–13	4	1, 2	1
S. plebeia	4	9–10	3	1, 2	1
S. bulleyana	2/4	13–15	3	2	1
S. dominica	4	11–13	4	1, 2, 3	1, 2
S. aegyptiaca	4	7–13	3	1, 2	1, 2

Table 1. Summary of variation. The numbers, except in the case of calyx veins, refer to those of the character states used by El- Gazzar et al. (1968).

The characters summarised above, except leaf indumentum, are illustrated in fig. 3. Two general features emerge from the table and the figure. First, there are clear differences between the species of each species-pair, except, on the basis of the used characters, *S. sylvestris* and *S. viridis*, and second, there is a considerable amount of intra-specific variation in the characters used. Examination of numerous gatherings both of the species cited above and others included in the sample showed that many of the multistate character variants used for at least the calyx and hair types were not at all clear-cut to recognise or define; yet between them they account for 26 of

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* *S. sylvestris* is a hybrid but from the data in the paper, it is likely that the plant meant is not *S. x sylvestris* but *S. nemorosa* L., one of its parents.

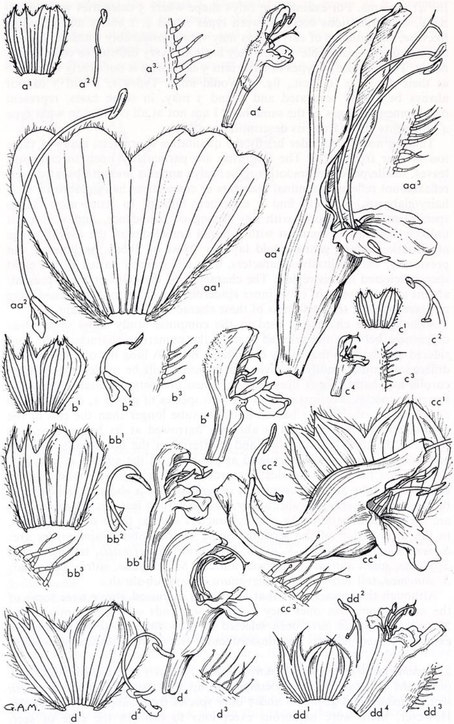

FIG. 3. Floral parts and indumentum types of *Salvia* species. Species within the same computer groups are given the same letter. Group 1: a^1–a^4, *S. verticillata*; aa^1–aa^4, *S. aurea*. Group 2: b^1–b^4, *S. sylvestris*; bb^1–bb^4, *S. viridis*. Group 4: c^1–c^4, *S. plebeia*; cc^1–cc^4, *S. bulleyana*. Group 6: d^1–d^4, *S. dominica*; dd^1–dd^4, *S. aegyptiaca*. 1, 2, 3 & 4 refer respectively to calyx, stamen, calyx indumentum and corolla. The floral parts are all x 2·5 and the indumentum of the calyces x c. 20.

the 41 variants. For example, in calyx shape where 5 categories were recognised, intergradations occur between types 1 and 4, 2 and 3 and 3 and 4; likewise, the number of calyx veins may vary considerably within a species, as in *S. aegyptiaca* (table 1), and they are often very difficult to count accurately. The division of types of hairs into 5 categories is not nearly so precise as their drawings (op. cit., fig. 3) would infer. Types 1, 2 and 3 cannot always be clearly separated and 2 and 3 may, in some cases, represent developmental stages of the same hair. I am not at all clear as to what type 4 represents either from its description or sketch.

Turning now to consider briefly the qualitative characters, many of these too are far from ideal. The following are particularly open to criticism: leaves, sessile/petiolate, smooth/rugose; calyx annulus present/absent; bracts reflexed/not reflexed; staminal filaments or connectives hairy/glabrous; style hairy/glabrous. I should find it extremely difficult to score most *Salvia* species on these features with any feeling of confidence, and it is most unlikely that any taxonomist with a broad knowledge of the overall range of variation in the genus would lay any stress on them. As pointed out previously, the qualitative characters, 9 in all, scarcely varied in the eight species selected in this review. The characters of the calyx-crystals, present/absent and cell walls of calyx inner epidermis thickened/not thickened were not investigated; the usefulness of these characters is still uncertain.

Although the characters used in the computer study show some clear differences between the selected species, the numerous characters not considered are the ones that really distinguish them. A long list of these further differences could readily be given but mention will be made only of two: corolla and habit. Fig. 3 illustrates the great diversity of floral structure in the eight species. For instance, in the two species of group 1, *S. verticillata* and *S. aurea*, the former has an annulate tube longer than the rest of the corolla and the upper hood is abruptly narrowed at its base whereas in *S. aurea* the tube is exannulate and shorter than the non-tubular portion and the hood is scarcely narrowed at the base; in the species of group 5, *S. dominica* has a broad falcate, scarcely bifid emarginate hood and an invaginated tube and in contrast *S. aegyptiaca* has a short straight deeply bifid hood and a straight tube. Many of these corolla features just mentioned are used, in association with other characters such as those of the stamens, in the delimitation of the sections. Some of the habit dissimilarities are: *S. verticillata*, erect herb, *S. aurea*, low shrub; *S. sylvestris*, tall perennial, *S. viridis*, small annual; *S. plebeia*, annual, *S. bulleyana*, sturdy perennial; *S. dominica*, tall sub-shrub, *S. aegyptiaca*, dwarf sub-shrub.

Although the species-pairs that have been discussed above were some of the more anomalous ones they do not form ends of a taxonomic series. Many others could have been selected to show that the seven groups are extremely heterogeneous and unsatisfactory from any biological viewpoint.

2. *Similar species.* In general, morphologically *closely* allied species did come out in the same groups. For example, group 3 contained only species from sect. *Eusphace* and groups 6 and 7 only species from subgenus *Calosphace*. However, there were numerous exceptions to this. In the case of sect. *Eusphace* most species were in group 3 but other members of the same section were placed in groups 1 and 4; *S. glutinosa* (sect. *Drymosphace*) was

in group 2 whereas the related *S. forskahlei* was in group 4; *S. dominica* (sect. *Gongrosphace*) was in group 5 and the species in the same general alliance such as *S. hierosolymitana* and *S. sclarea* were in group 2. Other similar examples could be cited in brief but the separation of *S. verbenaca* in group 2 from *S. controversa* in group 4 deserves a short discussion as they are undoubtedly close allies (Pugsley, 1927).

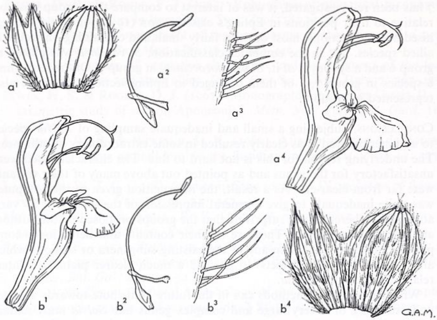

FIG. 4. a¹, calyx; a², stamen; a³, calyx indumentum and a⁴, corolla of *S. verbenaca* of the computer group 2. b¹, corolla; b², stamen; b³, calyx indumentum and b⁴, calyx of *S. controversa* of group 5. The floral parts are all x 2·5 and the indumentum of the calyces x c. 20.

A fairly large number of examples of these two species was examined and the characters covered in the previous Table are summarised in Table 2.

	Calyx type	Calyx veins: number	Stamen type	Calyx indumentum type	Leaf indumentum type	Leaf shape
S. verbenaca	4	13	4	1, 2	1	simple/divided
S. controversa	4	13	4	1, 3	1	divided

Table 2. Summary of character variation in *S. verbenaca* and *S. controversa*.

As the table shows, there is scarcely any difference at all between the two species; the only one in fact is the absence of hair type 2 in *S. controversa*. By the authors' definition of the two groups, however, they supposedly differ in calyx indumentum (*not* types 2 and 4 in group 5 which includes *S. controversa*) and leaf shape (simple in group 2 and divided in group 5), and in these characters only. But when a wide range of material of *S. verbenaca* and *S. controversa* is examined, as it was in this review, these differences just do not hold. The close similarities in calyx and corolla structure are shown in fig. 4. There is no doubt at all that these two species are very closely related and the only character that absolutely separates them is the presence of long lanate calyx hairs on *S. controversa* in contrast to the shorter hairs of the calyx of *S. verbenaca*.

Turning now to the subgenus *Calosphace*, the authors' recognition that its species are clearly different from those of the Old World only serves to support a fact that has been known since Bentham provided the initial generic classification in 1833. Although none of the species in groups 6 and 7 has been re-investigated, it was of interest to compare their group position relative to their positions in Epling's classification (1938–39). Epling recognised over 90 sections, most of them fairly small and containing only clearly allied species. Yet in the computer classification, *S. coccinea* was placed in group 6 and a synonym of it, *S. pseudococcinea*, in group 7. Of the remaining 8 species in group 7, 4 of them belonged to Epling sections that were also represented in group 6.

CONCLUSIONS. Subjecting a small and inadequate sampling of *Salvia* species to a numerical study has clearly resulted in some extraordinary misalliances. The underlying reason for this is not hard to find. The characters used were unsatisfactory for the genus and as pointed out above many of their variants were far from clear-cut. As a result, the information given to the computer was quite inadequate to give a general impression of the species or its variability. It is therefore not surprising that the groups proposed by the authors are totally unacceptable. They are by their contents and definition incomparably more artificial than any of the existing subgenera or sections which although not without defects do provide a much clearer picture of interrelationships within *Salvia*.

Whether computer methods can in the future contribute towards a better understanding of a very large and complex genus like *Salvia* must remain an open question. But one conclusion that must be drawn is that in any future study of *Salvia* ways would have to be found to codify the features of the corolla form in which much of the diversity of the genus is expressed.

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